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Genetic factors governing resistance and susceptibility of oats to Puccinia coronata avenae, Eriks & E Henn, race 57

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GENETIC FACTORS GOVERNING RESISTANCE AND SUSCEPTIBILITY OF OATS TO PUCCINIA CORONATA AVENAE, ERIKS. & E. HENN., RACE 57

by

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INTRODUCTION

Record or near record oat yields have been produced in Iowa in the past four years. One of the main factors contributing to these high yields has been the widespread use of new disease resistant varieties developed and released by state and federal experiment station workers. Yet, in 1949 crown rust, *Puccinia coronata avenae**, reduced the oat yields in Iowa by an estimated 12 percent. Yields in many sections of the country, particularilly in the South, were reduced to a considerably greater extent. Losses with these new varieties were due to changes in races of crown rust and to multiplication of those races which parasitize varieties resistant to formerly prevalent races.

The mechanism of reproduction of the pathogen is such that new and more virulent races can be expected to appear. The increase in prevalence of a new race depends upon the selection pressures provided by host plants. The hope of maintaining disease resistance in a crop then depends upon the location and transfer of genes for crown rust resistance to agronomically desirable varieties.

The most efficient and satisfactory method to attain this objective would be to catalogue sources of resistance to specific races and to determine the genetic factors carried by those sources as measured by host-parasite relationships. The known factor or factors can then be chosen and transferred with maximum efficiency either for development of more suitable parental material or for the production of desirable crown

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*Throughout the remainder of this thesis *Puccinia coronata* Corda, f. sp. *avenae* (Eriks. & E. Henn.) Eriks., will be referred to by the common name of crown rust.

rust resistant varieties.

It was the objective of this study to determine the differences in genotype for resistance to crown rust race 57 among a group of oat varieties based on a genetic analysis of segregating populations from crosses among the resistant varieties and to a susceptible variety. Such an analysis should yield information of value in an oat improvement program in which resistance to crown rust is a major objective.

REVIEW OF LITERATURE

Inheritance of Resistance to Crown Rust

Hoerner (9) first showed physiological specialization of crown rust by identifying four races by the use of two differential varieties. At the present time Murphy (16) has identified 95 races with the use of 13 differential varieties. Many inheritance studies have shown physiological specialization to be Mendelian in nature. Crown rust was shown to be heterothallic by Allen (1). New races of crown rust may arise by gene recombination or by mutation.

There are many sources of resistance to known races of crown rust among oat varieties. In addition to the differential varieties (any one of which could be considered as a source of resistance) there are many others which could and are being used.

All investigators, but two, have reported resistance dominant or partially dominant to susceptibility in the seedling plant. Parker (19) in a cross of Burt x Sixty-Day reported susceptibility dominant. Ko, Torrie and Dickson (11) reported a cross of Bond x S.D. 334 as segregating 15 susceptible to 1 resistant. A factorial interpretation was not given in either case.

Hayes, Moore and Stakman (8) in crosses involving the variety Bond, reported two independent dominant complementary factors conditioning the resistance of Bond. With similar crosses (Bond and/or derivatives of Bond assumed to carry the Bond type of resistance) these results were confirmed by Ko, Torrie and Dickson (11) for races 3 and

6, by Cochran, Johnston, Heyne and Hansing (2) for race 1, by Litzenberger (12) for race 1, by Weetman (25) for race 1 and again by Hayes (7).

Torrie (22) in a cross of Bond with Iowa N. 444 concluded that Bond has a single dominant factor pair for resistance.

Before the advent of Helminthosporium victoriae, Meehan and Murphy (14), the oat variety Victoria was a major source of resistance to crown rust. Several investigators have shown that Victoria carries a single dominant factor pair for resistance including Cochran, Johnston, Heyne and Hansing (2) for race 1, Litzenberger (12), Murphy, Stanton and Stevens (18) and Weetman (25) for race 45. Smith (21) did not give a genetic interpretation of results obtained from his crosses involving Victoria.

Litzenberger (12) reported that a single factor pair from the oat variety Landhafer conditioned resistance to races 1 and 45. Kehr and Hayes (10) reported resistance to races 1, 3, 4, 5, 6, 33, 57 and 68 as controlled by a single factor from Landhafer.

Weetman (25) found resistance from the oat variety Mutica Ukraine* to a major portion of race 1 to be due to two independent complementary dominant factors.

Dietz and Murphy (5) reported a single dominant factor pair conditioning resistance to race 33 from the varieties Sunrise 23, Red

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*The oat variety Ukraine has in previous literature been referred to as Mutica Ukraine and/or Mutica. The name Ukraine is now being used and will be used throughout the remainder of this thesis.

Rustproof and Algerian-Calcutta 89.

Davies and Jones (3) (4) reported a single dominant factor pair conditioning resistance of Red Rustproof to a single unidentified race of crown rust.

A dominant inhibitor factor from Fulghum epistatic to the dominant factor for resistance to race 33 from Sunrise 23 was reported by Dietz and Murphy (5). A dominant factor from Iowa No. 444 epistatic or partially epistatic to a dominant factor for resistance to races 1, 7, and 46 from Bond has been reported by Torrie (22). Cochran, Johnston, Heyne and Hansing (2) reported two independent dominant complementary inhibiting factors from Richland-Fulghum which were epistatic to the two independent dominant complementary factors of Bond for resistance to race 1.

Cochran, Johnston, Heyne and Hansing (2), Litzenberger (12) and Westman (25) have shown the Victoria and the two dominant complementary Bond factors to be independent. Litzenberger (12) has shown the two dominant complementary Bond factors to be independent of the Santa Fe factor. He also has shown Santa Fe to carry one or the other of the two dominant complementary Bond factors. Westman (25) assumed the two dominant complementary factors of Ukraine were alleles to the Bond factors. Litzenberger (12) suggested that the Landhafer and Santa Fe factors for resistance to crown rust were probably different.

Inheritance of Resistance to *H. victoriae*

H. victoriae was first described by Meehan and Murphy (14) in 1946. Murphy and Meehan (17) reported that the pathogen on oats parasitized only those oat varieties which have the Victoria type of crown rust resistance. From 248 oat selections all having the Victoria type of crown rust resistance all were susceptible to *H. victoriae*. In the F_2 population of 8 hybrids each of which involved Victoria as one of the parents the segregation for reaction to *H. victoriae* was three susceptible to one resistant while reaction to race 45 crown rust segregated 3 resistant (Victoria type) to one susceptible. They concluded the factors governing the Victoria type of crown rust resistance and susceptibility to *H. victoriae* were completely linked.

Litzenberger (12) in six crosses, two of which involved Victoria, came to the same conclusion. In one non-Victoria cross of Mindo x Landhafer some few progenies were susceptible to *H. victoriae*. He assumed this to be a result of natural crossing with a susceptible Victoria derivative.

Inheritance of Dwarfness

Dwarfs in oats, wheat and barley have been reported to occur beyond the F_2 in segregating generations of crosses between two normal varieties. Seldom do they occur in the F_2 from a normal F_1 of normal parents. Waldron (24) however, in a cross of Kota x Marquis wheat obtained segregation in the F_2 for dwarfness from a normal F_1 plant. He explained his results by assuming three factors, a factor for normal which was epistatic to factors for dwarfing and two dominant complementary factors for dwarfness. In order that his data fit this hypothesis he had to assume a labile condition of these factors.

Goulden (6) in a cross of the same varieties as used by Waldron (24) and also in a cross of Ghul x Marquis wheat explained his results on the basis of a dominant factor for dwarfing and a dominant inhibitor factor epistatic to the factor for dwarfing. Considerable abnormalities occurred, especially in Kota x Marquis, which increased the variability of the results.

Wakabayashi (23) in a cross of Red Rustproof x Black Tartarian oats, obtained 9.3 percent dwarf plants in the F_2 from a normal F_1. Among the F_2 segregation 51 percent produced some dwarf plants in their progenies. Very few true breeding dwarf plants were found and he accounted for this by assuming a high zygotic mortality rate in the dwarfs. He concluded dwarfness was not due to a single factor but suggested no other genetic hypothesis.

Litzenberger (12) in a cross of Mindo x Landhafer oats obtained dwarf plants in the F_2 from normal F_1's. In the F_3 two out of three of the F_3 lines segregated for dwarfness. He interpreted his results on a monogenic basis, but the gene action of such a basis was not given.

Inheritance of Marginal Hairs and Leaf Sheath Pubescence

Shaw and Bose (20) studied the inheritance of marginal hairs on the oat leaf in a cross of Scotch Potato x B. S. 2. Scotch Potato was classified as having numerous hairs, B. S. 2 as having few and the F_1 nearly intermediate between the two parents with partial dominance for numerous hairs. On the basis of F_2 and F_3 data they concluded the parents differed by two factor pairs, a dominant factor for the production of

MATERIALS AND METHODS

The parental varieties used in this study were furnished by Dr. H. C. Murphy and were as follows: (1) Klein 69b, C.I. 4118; (2) Trispernia, C.I. 4009; (3) Victoria, C.I. 2401; (4) Santa Fe, C.I. 4518; (5) Ukraine, C.I. 3259; (6) Landhafer, C.I. 3522; (7) Reselect Clinton, C.I. 5011; and (8) Anthony-Bond x Boone, C.I. 5220.

Of the possible 28 crosses, disregarding reciprocals, 22 were obtained in the greenhouse in the winter of 1948. A total of 79 F_1 seeds were obtained and the actual parents involved in each cross were maintained as individual lines.

The F_1 plants were grown individually in $2\frac{1}{2}$ inch clay pots in the greenhouse, tested with a mixture of races of crown rust and transplanted to one gallon glazed pots and grown to maturity.

Seed yields from the F_1 plants were not so good as expected, the average being only about 150 seeds per plant. These seeds were harvested in the late spring of 1948 and planted one seed per 2 inch paper pot. Due to considerable delayed germination the number of F_2 seedlings obtained was very small in most crosses. The seedlings were tested for rust reaction to a strain of rust to which the variety Ukraine was fully susceptible. After readings were obtained the seedlings were transplanted in the field. Due to the late date of planting and a drought condition during and following transplanting many of these plants died or failed to produce seed. The progeny from these plants were not further tested in this study.

The seeds that did not germinate were recovered from the pots and saved for planting the following year. It was interesting to note that seeds planted for as long as six weeks kept constantly wet and subjected to alternate freezing and thawing in an effort to break dormancy were in most cases still viable the following year.

In the late fall of 1949 the F_2 seeds were planted in the greenhouse. The collection of crown rust used the previous spring and all other collections of uredospores stored over the summer period were found to be non-viable. This was presumably due to freezing temperatures for a two day period in the cold vault where the rust spores were stored.

A collection of uredospores was made in a field of volunteer oats in an area of only about two square feet and where no other rust was present for a considerable distance. This collection* was increased and used for testing the F_2 seedling reactions.

Since greenhouse space was limited, approximately 100 F_2 individual plants from each cross were grown. In addition to the 22 crosses previously made, Dr. H. C. Murphy supplied F_2 seed of one additional cross.

The F_2 seeds were planted individually in $2\frac{1}{2}$ inch clay pots. Rust inoculations were made in the first leaf stage of plant growth by placing uredospores on the leaf, atomizing the leaf with water, and placing plants in a humidity chamber for a period of 24 hours. Rust reactions were recorded 12 to 14 days after inoculation. Seedling reactions were

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*This collection was predominantly crown rust races 45 and 57. The variety Ukraine was immune to this collection. The phrase "mixture of races" refers to this collection throughout this thesis. The race or mixture of races to which Ukraine was susceptible will be referred to as crown rust race Ukraine.

classed similar to the scale described by Murphy (15) and illustrated in Figure 1. In this study the immune and zero reaction types were classed separately. The Victoria type of crown rust reaction was also recorded in a separate class.

At the time crown rust reactions were determined each seedling was classified for leaf sheath pubescence in all crosses and for marginal leaf hairs in all crosses involving Victoria as one parent.

In the spring of 1950 it was decided to progeny test all F_2 plants with a pure race of rust. An effort was made to test at least 20 progenies of each F_2 plant. Due to unfavorable and crowded conditions under which the F_2 plants were grown and the lack of vigor in many of the crosses the F_3 seed produced was below expectations in many cases. Again delayed germination presented a problem as many of the plants were not ripe when it was necessary to harvest them. A satisfactory progeny test of many of the F_2 plants was not possible.

The F_3 seeds from individual F_2 plants were planted in 4 inch paper pots and inoculated with rust spores mixed with talcum powder, much the same as the method described by Murphy (15). A mixture of 1 part rust to 50 parts talc was used and heavy infection resulted. A rust reading was taken on each individual F_3 plant 10 to 14 days after inoculation depending upon the cross and weather conditions.

All crosses involving Victoria were tested for reaction to _H. victoriae_ after they had been tested for rust reaction. The method used was similar to that described by Litzenberger (13) and seedlings were classified as being resistant or susceptible. After crown rust or crown rust and _H. victoriae_ readings had been made the plants were transplanted

Figure 1. Infection types of crown rust.

Left to right (1) zero "0" type of pronounced necrotic flecks of lesions; (2) one "1" type of minute uredia surrounded by solid necrotic areas; (3) two "2" type of small uredia with hypersensitive areas varying from sharp necrosis to pronounced chlorosis; (4) three "3" type of medium size uredia with chlorosis but no necrosis considered moderately susceptible; (5) four "4" type of large confluent uredia considered as fully susceptible.

The immune type "I", Victoria type "V", and the mesothetic "X" type reactions are not shown here.

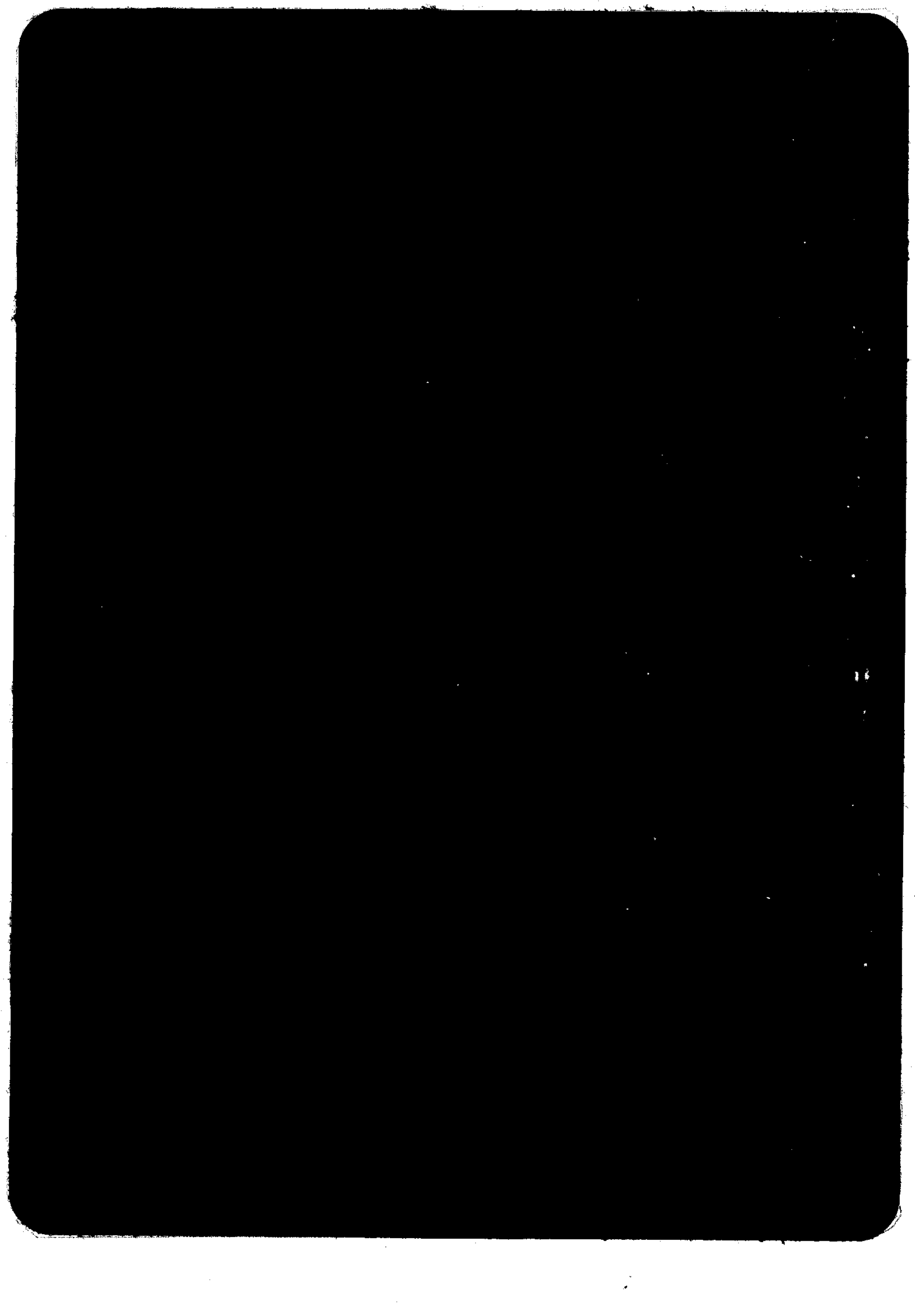
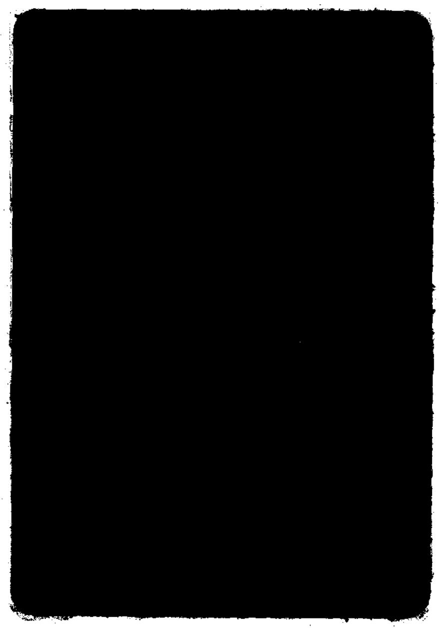
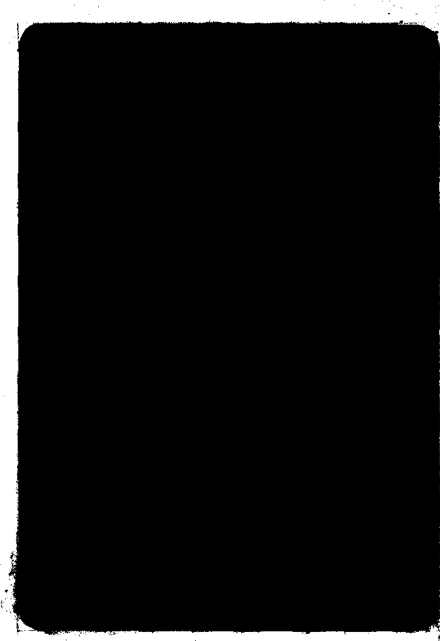


Figure 2. Reaction of the thirteen differential varieties and eight other sources of resistance to a mixture of crown rust races.

Upper left. Left to right. (1) Susceptible, (2) Susceptible, (3) Mesothetic, (4) Mesothetic, (5) Susceptible. Upper right. (6) Resistant, (7) Mesothetic, (8) Mesothetic, (9-10) Susceptible. Lower left. (11-12) Susceptible, (13) Resistant, (14) (Landhafer) Resistant, (15) (Santa Fe) Resistant. Lower right. (16) (Ukraine) Resistant, (17) (Trispernia) Resistant, (18) (Clinton) Susceptible, (19) (Santa Fe x Clinton) Resistant, (20) (Anthony-Bond x Boone) Resistant.





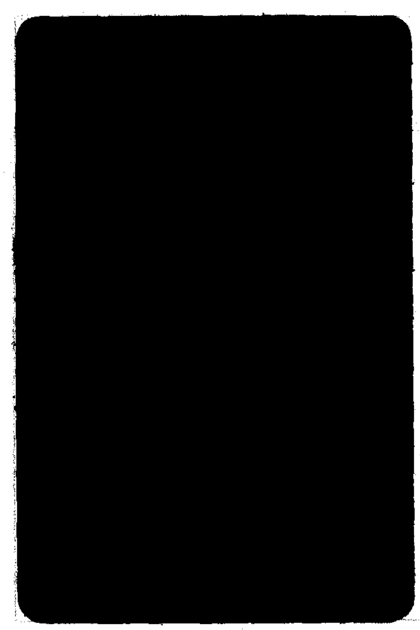
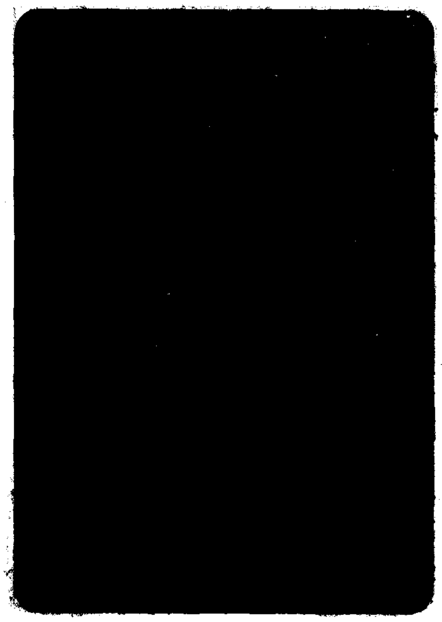
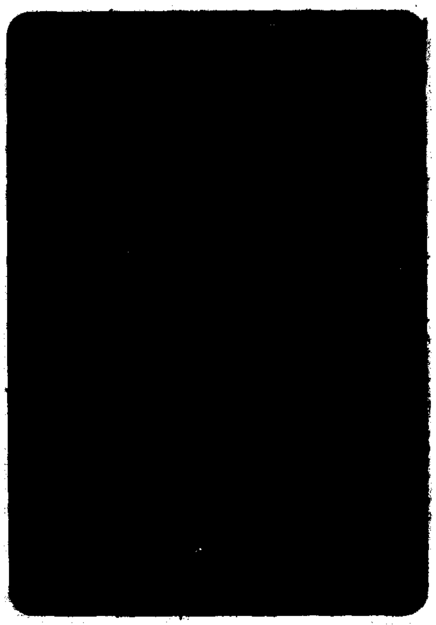
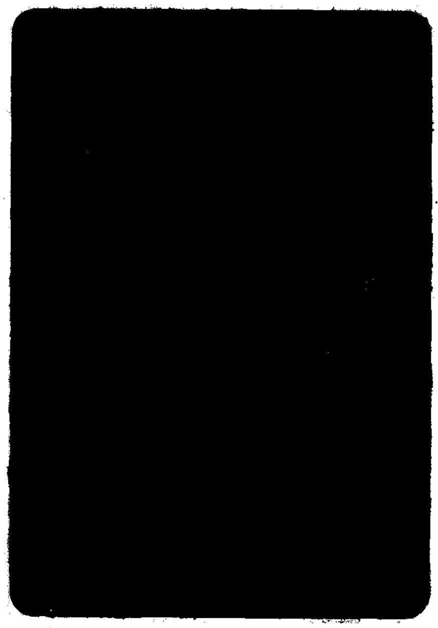


Figure 3. Reaction of the thirteen differential varieties and eight other sources of resistance to crown rust race 57.

Left to right. Upper left. (1) Resistant, (2-5) Susceptible. Upper right. (6) Resistant, (7-10) Susceptible, Lower left. (11-12) Susceptible, (13) Resistant, (14) (Landhafer) Resistant, (15) (Santa Fe) Resistant, Lower right. (16) (Ukraine) Resistant, (17-18) (Trispernia) Variable resistant reaction,(19) (Reselect Clinton) Susceptible, (20) (Santa Fe x Clinton) Resistant, (21) (Anthony-Bond x Boone) Resistant.







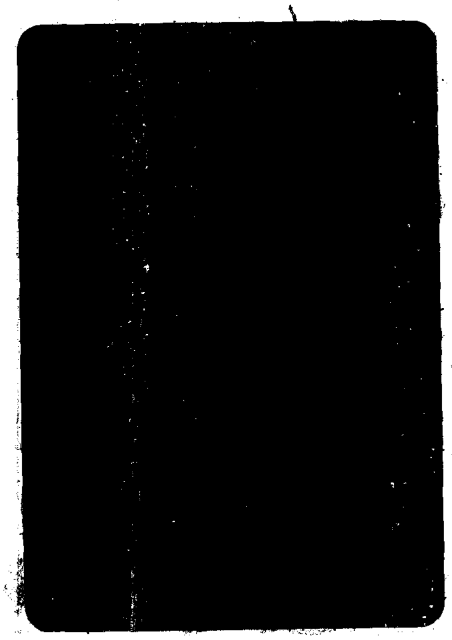


Table 1. Pathogenicity of crown rust strains and collections used in this study to the thirteen standard differential varieties.

Differential variety	C.I. No.	Race Ukraine	Mixture of races	Race 57
1. Ruakura	2025	3	3	2
2. Green Russian	2890	3	4	3
3. Hawkeye	2264	0 - 2	4 - 0	4
4. Anthony	2143	0 - 2	4 - 0	3
5. Sunrise	982	3	4	4
6. Victoria	2401	2	2	2
7. Green Mountain	1892	1 - 3	4 - 0	4
8. White Tartar	551	1	4 - 0	3
9. Appler	1815	4	4	4
10. Sterisel	2991	4	4	4
11. Belar	2760	3	4	4
12. Bond	2733	3	4	4
13. Glabrota	2630	0	0	0

to the field.

In the spring of 1950 most of the remaining F_2 seeds were planted and the seedlings tested for crown rust reaction. The seeds were planted individually in 2 inch paper pots and transplanted to the field after crown rust reaction had been recorded.

All soil used was treated for a period of 8 to 12 hours in a steam oven without pressure, at a temperature of about 180°F. Soil used for growing crosses involving Victoria as one of the parents was sterilized in a steam autoclave for several hours under 15 lbs. pressure.

Dwarf and albino plants were noted whenever the opportunity arose. Although there were many other contrasting characters and apparent abnormal segregates, a study of their inheritance was beyond the scope of this investigation and detailed notes were not taken on these characters.

The crown rust reaction types of the standard differential varieties to the rust strains used in these studies are given in Table 1. The rust strain to which Ukraine was susceptible was increased on the variety Ukraine but produced a mesothetic type reaction on some of the differentials. Photographs of the crown rust reactions of the standard differential varieties are shown in Figure 2 to the mixture of races used to study many of the F_2 seedling reactions. Photographs of the rust reaction of the standard differential varieties for race 57 are shown in Figure 3.

EXPERIMENTAL RESULTS

Parents and F_1's

Photographs of the crown rust reaction of parental progenies to race 57 crown rust are shown in Figures 4, 5, 6 and 7. The parental reactions to a mixture of races were determined on the basis of a single plant while the reaction to race 57 was determined on the basis of several. The reactions of the F_1 seedlings were determined for a mixture of races (predominantly races 45 and 57 including biotypes to which Ukraine was susceptible).

The variety Klein 69b was inconsistent and mesothetic in crown rust reaction in the greenhouse. Reactions on the same leaf varied from 0 to large susceptible pustule type. Pustules generally were surrounded by a necrotic area or by a green area which in turn was surrounded by a necrotic area.

The variety Trispernia was found to be a mixture of genotypes some being more resistant than others. The parents 2B-1, 2-23 and 2B-27 were less resistant than were the other parent plants in this variety. The average reading given the variety Trispernia was a 2 type.

The variety Victoria and the actual parental progenies were consistent in crown rust reaction. However, there was considerable variation in the Victoria reaction under different environmental conditions.

Santa Fe reacted consistently with the exception of parent 4-15 which was not as resistant as the others. The reaction of Santa Fe varied from a 0 to a 1 for race 57 depending upon the environmental

Figure 4. Reaction of progenies of actual parents used in this study to crown rust race 57.

Left to right. Left half. Variety Klein 69b plants 7, 17 and 24. Right half. Variety Trispernia plants 12, 22, 23 and 27. All plants were classified resistant.

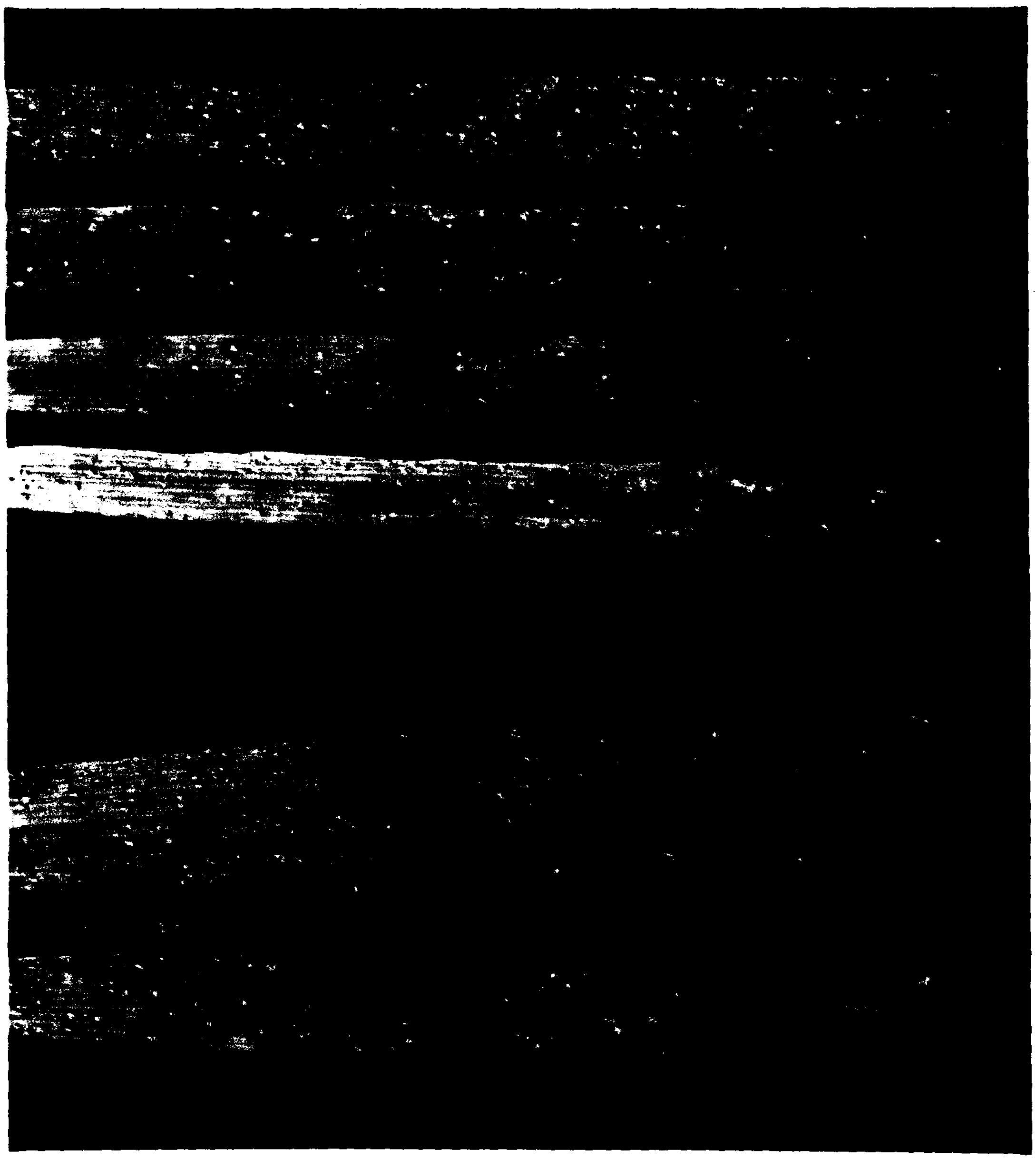


Figure 5. Reaction of progenies of actual parents used in this study to race 57 crown rust.

Left to right. Left half. Variety Victoria plants 5, 8, 9 and 11. Right half. Variety Santa Fe plants 3, 4, 7, 11 and 16. All plants were classified resistant.

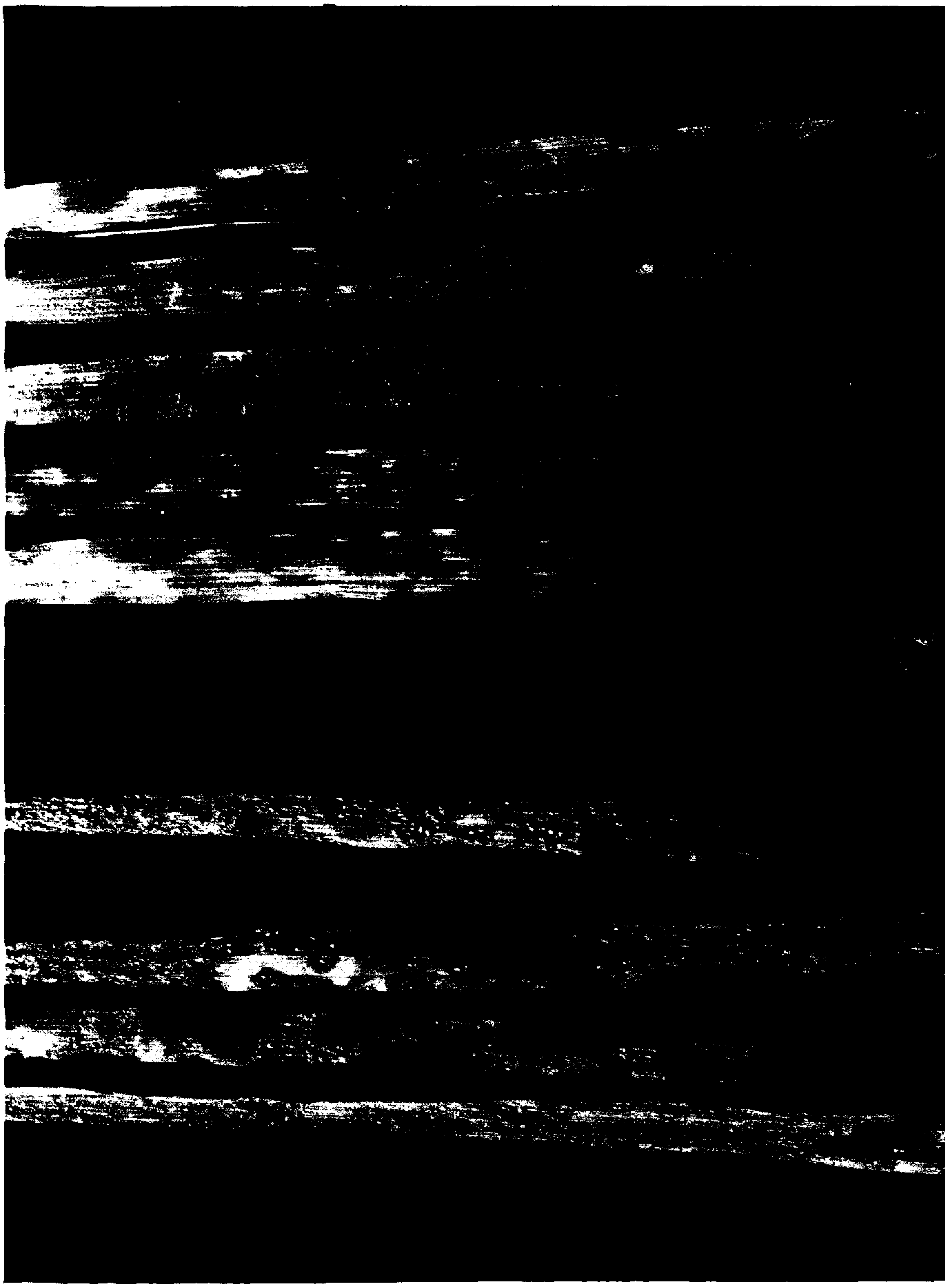


Figure 6. Reaction of progenies of actual parents used in this study to race 57 crown rust.

Left to right. Left half. Variety Ukraine plants 2, 3, 18, 24 and 26. Right half. Variety Landhafer plants 2, 6, 16, 22 and 23. All plants were classified resistant.

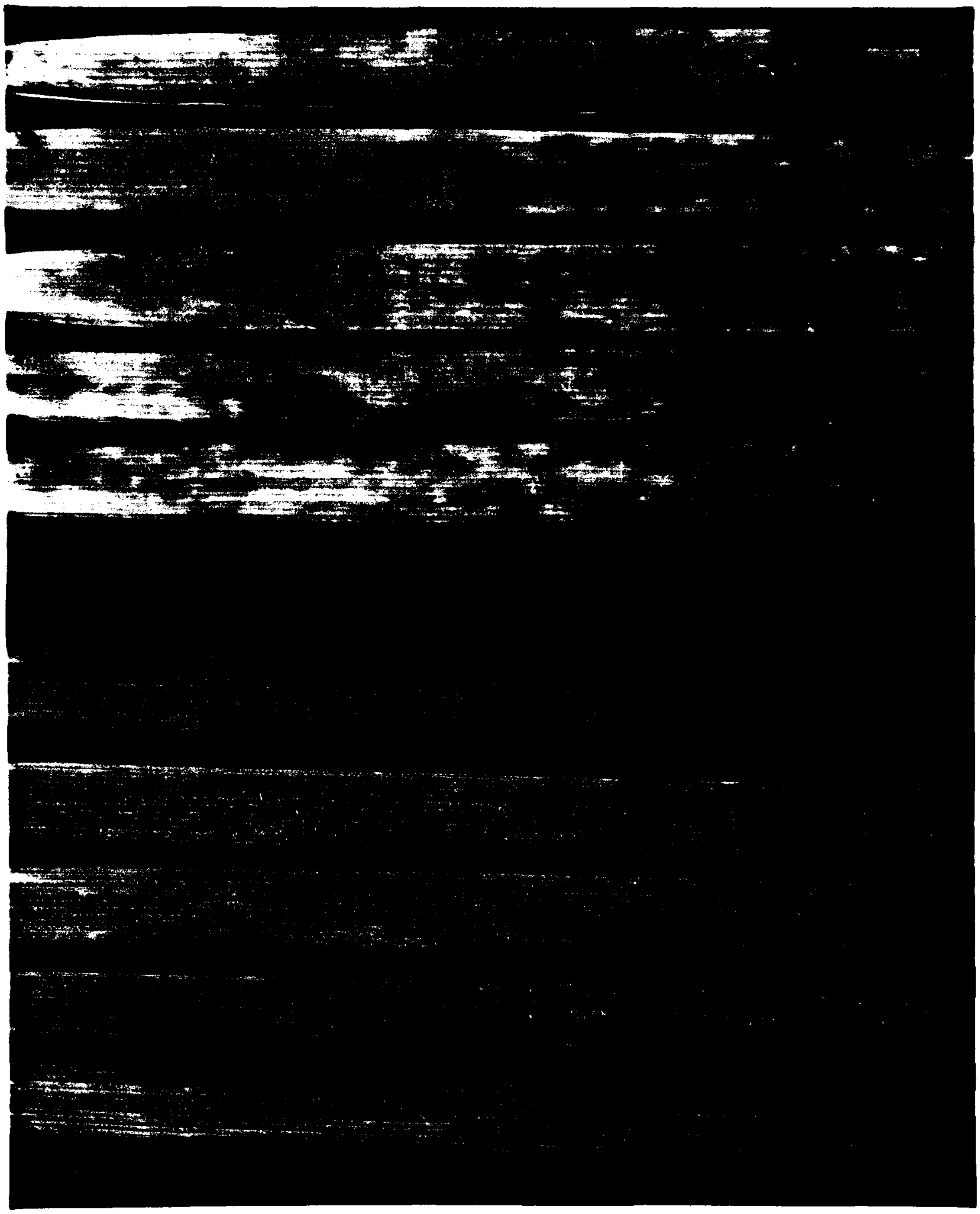
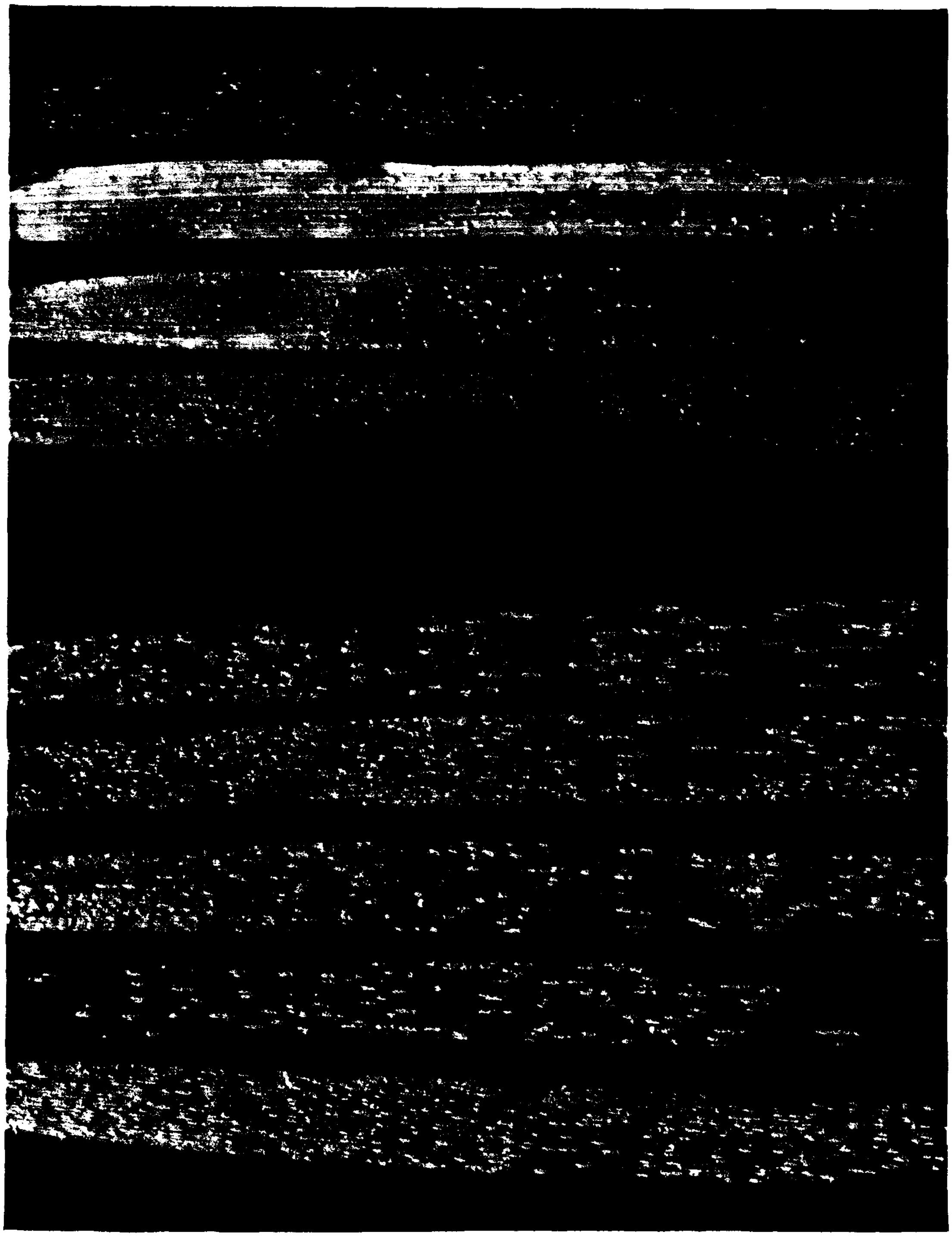


Figure 7. Reaction of progenies of actual parents used in this study to race 57 crown rust.

Left to right. Left half. Variety Reselect Clinton plants 8, 11, 17, 21 and 163. Right half. Variety Anthony-Bond x Boone plants 2, 4, 6 and C.I.5220. All plants of the variety Reselect Clinton were classified as susceptible and all plants of the variety Anthony-Bond x Boone were classified as resistant.



conditions under which the seedlings were tested.

The variety Ukraine was known to be susceptible to biotypes of several races. It was not suprising that it yielded variable results when inoculated with a mixture of races. The progenies of one parental plant, 5-17, were found to be fully susceptible to race 57. Progenies of other parental plants showed immunity, an extreme type of resistance to race 57.

Landhafer was characteristically resistant to race 57, showing a 0 type of reaction. The Landhafer reaction also varied from a 0 to a 1 type with changes in environment. Progenies of parent 6-4 proved to be fully susceptible. The occurrence of this plant probably was the result of a natural cross at some earlier time. Parent 6-9 was evidently a natural hybrid between Landhafer and some susceptible variety as the progenies of the actual parent segregated in a ratio approximating a 1:2:1.

All parent progenies of Reselect Clinton were fully susceptible.

The parental progenies from Anthony-Bond x Boone were on the border between resistance and susceptibility in reaction to race 57 in the greenhouse.

In most cases the F_1 reaction was intermediate of the parental reactions, indicating partial dominance of factors for crown rust resistance.

Crosses of Resistant x Susceptible Parents

Crosses between resistant and susceptible varieties were expected to yield information on the number of factor pairs involved and the type of gene action determining resistance and susceptibility to a specific race of crown rust.

Ukraine x Clinton, cross # 55

The cross of Ukraine x Clinton involved the extremes in rust reaction types, Ukraine being immune and Clinton fully susceptible to race 57. A photograph of the progeny of the actual parents and the F_2 segregation is shown in Figure 8.

On the basis of the F_2 data, corrected* by progeny tests, the following segregation was obtained: 50 bred true for Ukraine type of resistance, 67 segregated into parental types and 21 bred true for susceptibility. It is evident that an assumption of linkage is needed to explain these results.

By assuming that Ukraine carried two linked factor pairs for resistance (MM UU), each being dominant, and each being capable of producing the Ukraine type of resistance, the linkage was estimated from the corrected F_2 data. It should be pointed out that not all the crossover types could be distinguished from the non-crossover types even by the

*The phenotypic rust classification of the F_2 individual plants was confirmed or corrected according to their breeding behavior in the following generation. The classification of these progeny tested F_2 plants was then a genotypic classification as well as a phenotypic classification. Wherever this procedure was used the word "corrected" F_2 data was used in this thesis. Where this procedure was not used the word "corrected" was omitted.

progeny test. The best linkage estimate could be made on the basis of the three identifiable corrected F_2 classes.

The estimation of linkage intensity was made by using the maximum likelihood procedure. This estimate was 23 percent crossing over or the gametic frequency of each parental gamete 38.5 percent and of each cross-over gamete 11.5 percent. The genotypic classes with their expected frequencies, breeding behavior, observed numbers and expected numbers based on the gene action and linkage intensity given are shown in Table 2. The breeding behavior showed the three classes could be identified on the basis of the F_2 readings indicating partial dominance for resistance.

The process of estimation used one degree of freedom leaving one remaining to test the goodness of fit. Where the numbers 48.6 : 69 : 20.4 were expected 50 : 67 : 21 were observed. This is obviously a good fit. A more critical test of this hypothesis in this cross was obtained from the comparison of observed and expected numbers of resistant and susceptible individuals in the segregating portion of the population. These data were not used in the estimation of linkage but only two classes could be recognized therefore only one degree of freedom was available to test for goodness of fit.

In the progenies from the segregating portion of the F_2 population it was expected 64.8 percent to be of the genotype Mm Uu. Of these 91.4 percent were expected to be in the coupling phase and segregate 85.2 percent resistant : 14.8 percent susceptible. The 8.6 percent in the repulsion phase were expected to segregate 98.7 percent resistant : 1.3 percent susceptible. The segregation of this class was therefore expected to be 86.3 percent : 13.6 percent. In the other two genotypes

Figure 8. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant and susceptible parents.

Left half. Ukraine x Reselect Clinton, cross # 55. Left to right. Ukraine parent (5-26)[1], F_2 plant 01[2], 1, 101, 401 and Clinton parent (7-17).

Right half. Landhafer x Reselect Clinton, cross # 89. Left to right. F_2 plants 101, 201, 202 and 401.

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[1]The first number refers to a particular variety while the second number refers to the plant within that variety used as a parent.

[2]The F_2 plants and F_3 lines were numbered according to their F_2 rust reaction types, i.e., 01, 02 etc. = immune type plant No. 1, 2 etc.; 1,2 etc. = "0" type plant No. 1, 2 etc.; 101, 102 etc. = "1" type plant No. 1, 2 etc.; 201, 202 etc. = "2" type plant No. 1, 2 etc.; 301, 302 etc. = "3" type plant No. 1, 2 etc.; 401, 402 etc. = "4" type plant No. 1, 2 etc. See Figure 1 for description of rust type.

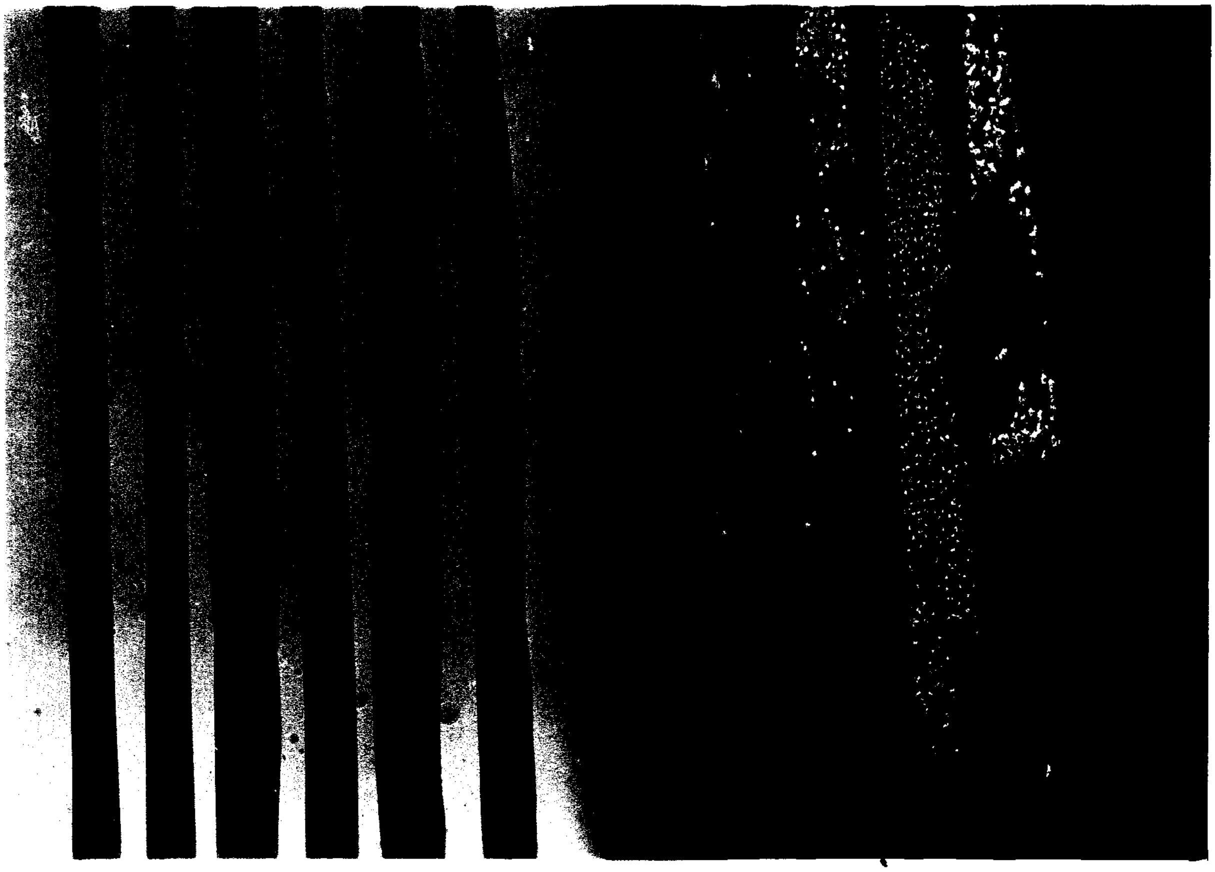

Table 2. Expected and observed frequency of phenotypic and genotypic classes based on corrected F_2 data for the cross Ukraine x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 5-26	Resistant	$\frac{M\ U}{M\ U}$ C.O.= 23%	Resistant			
Male Parent 7-17	Susceptible	$\frac{m\ u}{m\ u}$	Susceptible			
F_1	Resistant	$\frac{M\ U}{m\ u}$	Segregate			
F_2	Resistant	$\frac{M\ U}{M\ U}$	Resistant	14.8		
F_2	Resistant	$\frac{M\ U}{M\ u}$	Resistant	8.8		
F_2	Resistant	$\frac{M\ u}{M\ u}$	Resistant	1.3	48.6	50
F_2	Resistant	$\frac{M\ U}{m\ U}$	Resistant	8.8		
F_2	Resistant	$\frac{m\ U}{m\ U}$	Resistant	1.3		
F_2	Resistant	$\frac{M\ U}{m\ u}$	Segregate	29.8		
		$\frac{M\ u}{m\ U}$	Segregate	2.6	69.0	67
F_2	Resistant	$\frac{M\ u}{m\ u}$	Segregate	8.8		
F_2	Resistant	$\frac{m\ U}{m\ u}$	Segregate	8.8		
F_2	Susceptible	$\frac{m\ u}{m\ u}$	Susceptible	14.8	20.4	21

(35.2 percent) the segregation was expected to be 75 percent : 25 percent. The total segregation was therefore expected to be 82.3 percent : 17.7 percent. From a total of 1,858 F_3 plants the expected numbers were 1,529.1 : 328.9 and the observed were 1542 : 316. This was a satisfactory agreement with the hypothesis.

Landhafer x Clinton, cross # 89

This cross involved the 0 - 1 Landhafer type reaction with the fully susceptible Clinton type. A photograph of the F_2 segregation observed in this cross is shown in Figure 8.

The data suggested that the parents differed by a single partially dominant factor pair for resistance to crown rust; the genes (LL) from the Landhafer parent and the recessive alleles (ll) from the Clinton parent. The F_2 genotypes and the expected and observed numbers are shown in Table 5 for the corrected F_2 data.

On the basis of the corrected F_2 data from a total of 72 seedlings the observed segregation gave a satisfactory fit to a 1 : 2 : 1 ratio. The segregating portion of the F_3 population had a total of 471 seedlings. The expected numbers on a 1 : 2 : 1 basis were 117.75 : 235.5 : 117.75 and the observed numbers were 128 : 185 : 158. This was not a satisfactory fit and may have been due to misclassification resulting from partial dominance.

Klein 69b x Clinton, cross # 18

This cross was between the resistant but variable crown rust

Table 3. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 data for the cross Landhafer x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 6-22	Resistant	LL	Resistant			
Male Parent 7-11	Susceptible	ll	Susceptible			
F_1	Resistant	Ll	Segregate			
F_2	Resistant	LL	Resistant	25	18	14
F_2	Resistant	Ll	Segregate	50	36	38
F_2	Susceptible	ll	Susceptible	25	18	20

reaction type of Klein 69b and the fully susceptible crown rust type of Clinton. The reaction of Klein 69b was mesothetic in the greenhouse* to both the mixture of rust races and to the pure race 57 so classification was difficult. A photograph of progeny of the actual parents and the segregation obtained in the F_2 is shown in Figure 9.

The data from this cross suggested the presence of a dominant inhibitor factor pair (I_kI_k) in Clinton which was epistatic to the dominant factor pair (KK) for resistance from Klein 69b. On the basis of this assumption the expected and observed numbers of the different genotypes (corrected F_2 data) are shown in Table 4.

With this assumption it was expected that from the progenies of 113 F_2 plants 49.4 would breed true susceptible, 56.5 would segregate and 7.1 would breed true resistant. A corresponding ratio of 51 : 55 : 7 was observed. The observed ratio gave a satisfactory fit to this hypothesis.

From the segregating portion of the F_2 a ratio of 3 susceptible : 1 resistant was expected in the F_3. From a total of 730 F_3 seedlings the observed numbers were 424 susceptible : 306 resistant where the expected numbers were 547.5 : 182.5. This was a very poor fit. The portion with the assumed genotype Kk i_ki_k segregated 167 resistant : 47 susceptible where 160.5 : 53.5 was expected. This was a satisfactory fit. It was in the classes KK I_ki_k and Kk I_ki_k where the major portion of the discrepancies were found. This was probably due to the incomplete epistasis of

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*The reader is referred to page 146 concerning the field vs. greenhouse reaction of Klein 69b.

Figure 9. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant and susceptible parents.

Left half. Klein 69b x Reselect Clinton, cross # 18. Left to right. Reselect Clinton (7-8), F_2 plants 301 and 401, Klein 69b (1-24).

Right half. Trispernia x Reselect Clinton, cross # 78. Left to right. Trispernia (2B-27), F_2 plants 201, 202, 301 and 401, Reselect Clinton (7-21).

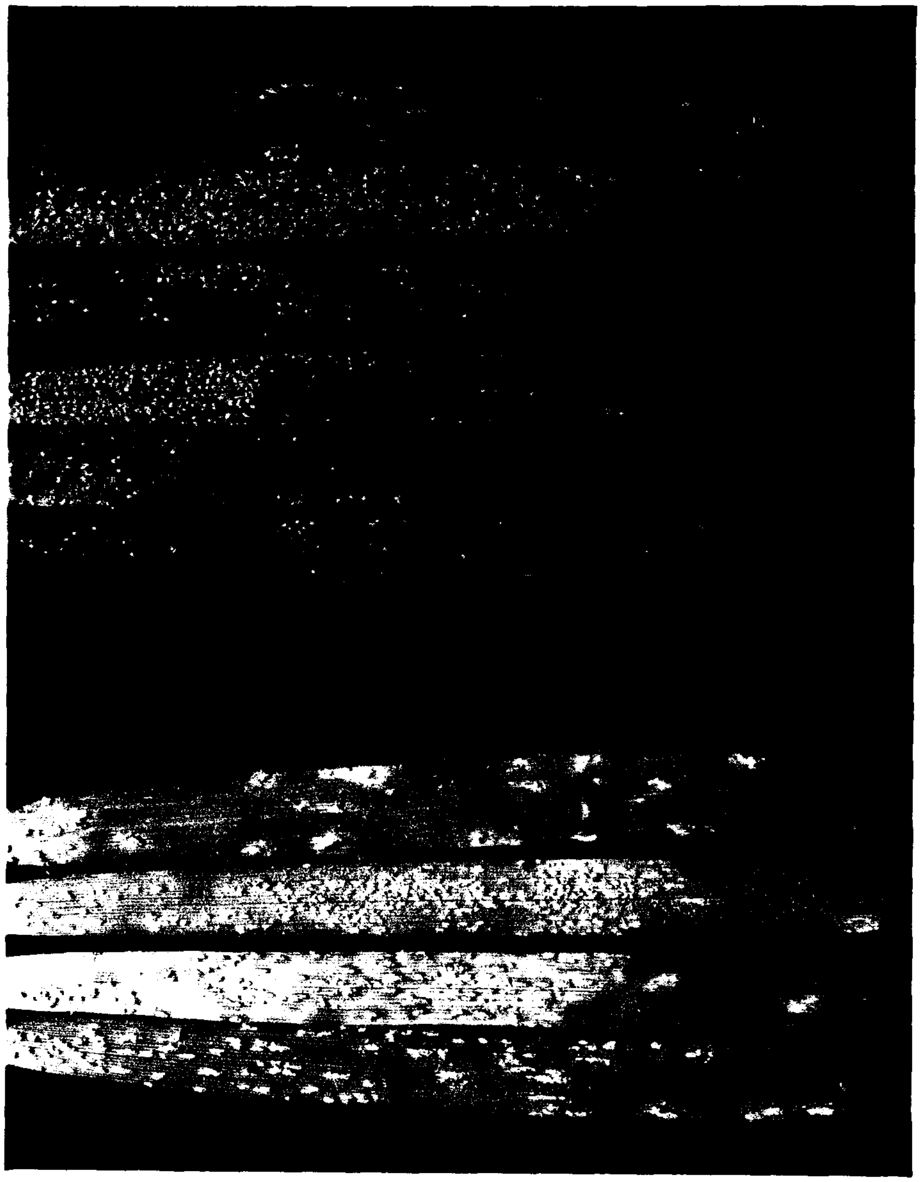

Table 4. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data for the cross Klein 69b x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 1-24	Resistant	KK $i_k i_k$	Resistant			
Male Parent 7-8	Susceptible	kk $I_k I_k$	Susceptible			
F_1	Susceptible	Kk $I_k i_k$	Segregate			
F_2	Susceptible	KK $I_k I_k$	Susceptible	6.25		
	Susceptible	Kk $I_k I_k$	Susceptible	12.50	49.4	51
	Susceptible	kk $I_k I_k$	Susceptible	6.25		
	Susceptible	kk $i_k i_k$	Susceptible	12.50		
	Susceptible	KK $I_k i_k$	Segregate	12.50	42.4	40
	Susceptible	Kk $I_k i_k$	Segregate	25.00		
	Resistant	Kk $i_k i_k$	Segregate	12.50	14.1	15
	Resistant	KK $i_k i_k$	Resistant	6.25	7.1	7

the heterozygous inhibitor factor over the factor for resistance.

Trispernia x Clinton, cross # 78

A photograph of the actual parents and the F_2 segregation of this cross is shown in Figure 9.

The corrected F_2 data indicated the parents differed by three factor pairs as shown in Table 5. On the basis of three independent factor pairs of which any one factor could give some degree of resistance, it was expected 57.8 percent to breed true resistant, 40.6 percent to segregate resistant and susceptible and 1.6 percent to breed true susceptible. From corrected data on 148 F_2 plants the expected numbers were 85.6 : 60.1 : 2.3. The observed numbers were 87 : 56 : 5 which was a satisfactory fit.

From the segregating portion of the population a ratio of 96.4 percent resistant to 3.6 percent susceptible F_3 seedlings was expected. The observed data did not agree with the expected. Partial dominance made it impossible to separate seedlings with one factor for resistance from the fully susceptible seedlings.

Victoria x Clinton, cross # 34 L

This was a cross between a resistant variety (Victoria) and a susceptible variety (Clinton). A photograph of the F_2 segregation is shown in Figure 10.

Only one factor pair for resistance was involved in this cross. The factor pair VV from Victoria was dominant over its recessive alleles in

Table 5. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust reaction data for the cross Trispernia x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 2B-27	Resistant	M_2M_2 V_1V_1 TT	Resistant			
Male Parent 7-21	Susceptible	mm vv tt	Susceptible			
F_1	Resistant	M_2m V_1v Tt	Segregate			
F_2	Resistant	M_2M_2 -- --	Resistant	57.8	85.6	87
	Resistant	V_1V_1 -- --	Resistant			
	Resistant	TT -- --	Resistant			
	Resistant	M_2m V_1v Tt	Segregate	40.6	60.1	56
	Resistant	M_2m V_1v tt	Segregate			
	Resistant	M_2m vv Tt	Segregate			
	Resistant	M_2m vv tt	Segregate			
	Resistant	mm V_1v Tt	Segregate			
	Resistant	mm V_1v tt	Segregate			
	Resistant	mm vv Tt	Segregate			
	Susceptible	mm vv tt	Susceptible	1.6	2.3	5

Clinton. On the basis of the corrected F_2 data as shown in Table 6, 34 plants bred true resistant, 64 segregated in the F_3 and 27 bred true for susceptibility where the expected numbers were 31.2 : 62.5 : 31.2. A chi square value 0.9 with a probability between 0.5 and 0.3 indicated a good fit.

In the segregating portion of the population 979 rust resistant F_3 plants to 385 susceptible F_3 plants were observed where the expected numbers were 1023 : 341. A chi square value of 7.6 was obtained with a probability of less than 0.01. In a sample as large as this better agreement of the observed with the expected was desired.

<u>Santa Fe x Clinton, cross # 46</u>

Santa Fe generally gave a 0 type reaction although under some conditions it did show a 1 type. Clinton is fully susceptible and a photograph of F_2 segregation of this cross is shown in Figure 10.

Assuming a single partially dominant factor pair (M_1M_1) for resistance from Santa Fe and its recessive allel from Clinton a 1 : 2 : 1 ratio was expected from the corrected F_2. On the basis of corrected F_2 data on 116 plants, a ratio of 43 : 47 : 26 was observed where 29 : 58 : 29 was expected as shown in Table 7. This was an unsatisfactory fit to the expected 1 : 2 : 1 ratio. A satisfactory fit to the ratio 3 breeding true resistant or segregating : 1 breeding true susceptible was obtained. The expected numbers were 87 : 29 and the observed numbers were 90 : 26. The numbers within a progeny apparently were not large enough to adequately separate the true breeding resistant and the segregating genotypes.

Figure 10. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant and susceptible parents.

Left half. Victoria x Reselect Clinton, cross # 34. Left to right. F_2 plants V202[1], V308, V401, 305, 405.

Right half. Santa Fe x Reselect Clinton, cross # 46. Left to right. F_2 plants 1, 111, 201, 301 and 413.

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[1]The letter "V" refers to a Victoria type crown rust reaction.

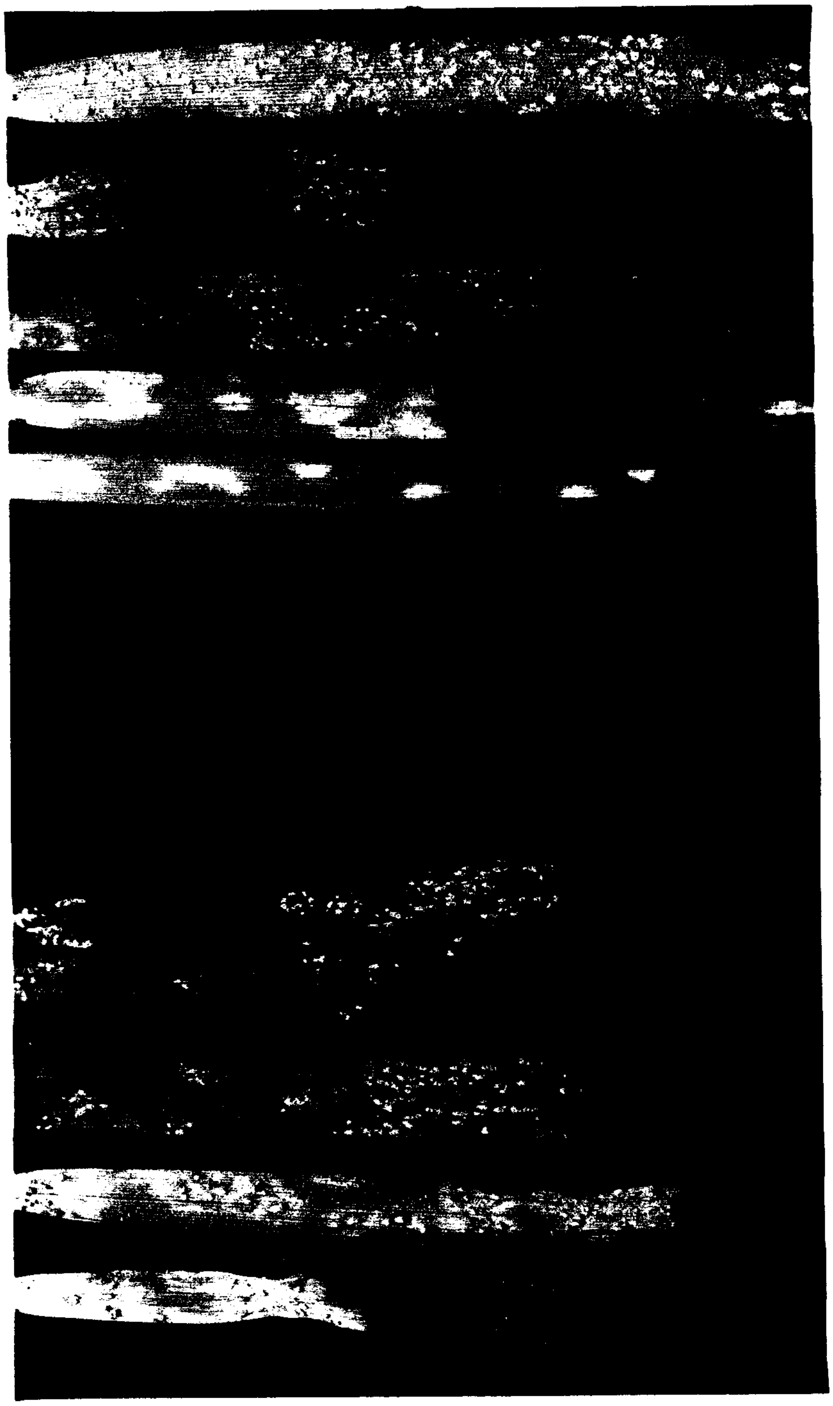


Table 6. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from a cross of Clinton x Victoria.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 7-11	Susceptible	vv	Susceptible			
Male Parent 3-9	Resistant	VV	Resistant			
F_1	Resistant	Vv	Segregate			
F_2	Resistant	VV	Resistant	25	31.2	34
	Resistant	Vv	Segregate	50	62.5	64
	Susceptible	vv	Susceptible	25	31.2	27

Table 7. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from a cross of Santa Fe x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 4-12	Resistant	M_1M_1	Resistant			
Male Parent 7-21	Susceptible	mm	Susceptible			
F_1	Resistant	M_1m	Segregate			
F_2	Resistant	M_1M_1	Resistant	25	29	43
	Resistant	M_1m	Segregate	50	58	47
	Susceptible	mm	Susceptible	25	29	26

In the segregating portion of the population where again a 1 : 2 : 1 ratio (partial dominance for resistance made it possible to distinguish the heterozygous and homozygous plants) was expected or from a total of 938 F_3 plants the expected was 234.5 : 469 : 234.5 and 266 : 482 : 190 was observed. A chi square value of 13.03 with 2 degrees of freedom indicated a probability of less than 0.01. The classification was not absolute enough to obtain a satisfactory fit.

Clinton x (Anthony-Bond x Boone), cross # 164

The actual parent of the resistant variety was not available. A photograph of the rust reaction of the variety (A.-B. x Boone), the actual Clinton parent and the F_2 segregation of the cross is shown in Figure 11.

From the corrected F_2 data on 124 plants the observed numbers were 62 bred true resistant, 56 segregated resistant and susceptible and 6 bred true susceptible as shown in Table 8. According to a hypothesis of two independent factor pairs, each partially dominant and capable of producing a resistant reaction, the expected numbers were 54.2 to breed true for resistance, 62 to segregate resistant and susceptible and 7.8 to breed true susceptible. On this basis agreement between the observed and expected was good.

In the segregating portion of the population the observed ratio was 775 resistant to 169 susceptible where the expected was 849.6 : 94.4. The data indicated that partial dominance for resistance led to misclassification where the progeny test was not used.

Figure 11. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in a cross between resistant and susceptible parents.

(Anthony-Bond x Boone) x Reselect Clinton, cross # 164. Left to right. Anthony-Bond x Boone C.I. 5220; F_2 plants 301 and 401; Reselect Clinton (7-163).

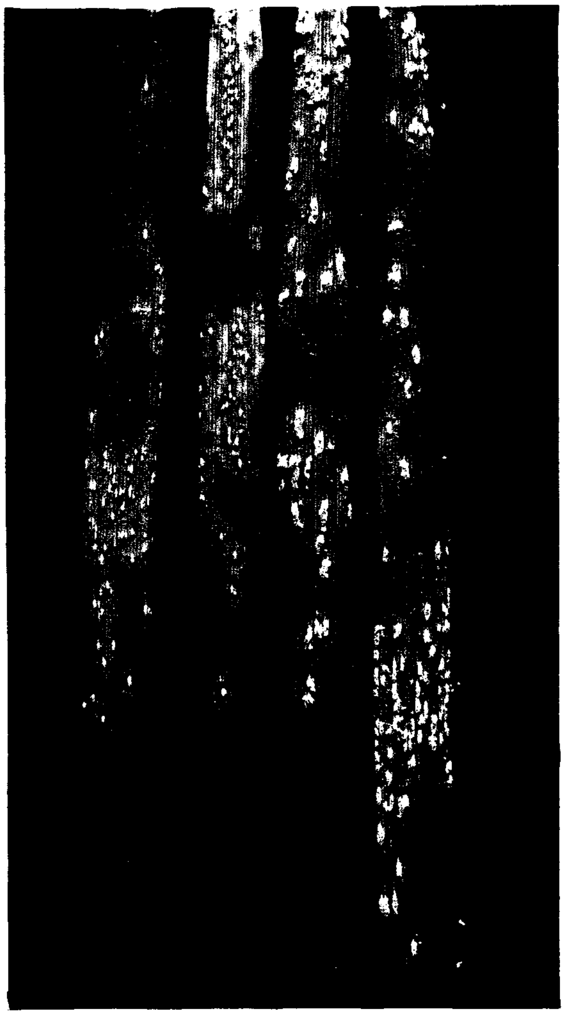


Table 8. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from a cross of Clinton x (Anthony-Bond x Boone).

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 7-163	Susceptible	mm vv	Susceptible			
Male Parent C.I. 5220	Resistant	M_2M_2 V_1V_1	Resistant			
F_1	Resistant	M_2m V_1v	Segregate			
F_2	Resistant	M_2M_2 --	Resistant	21.875	54.2	62
	Resistant	V_1V_1 --	Resistant	21.875		
	Resistant	M_2m V_1v	Segregate	25.0	62.0	56
	Resistant	M_2m vv	Segregate	12.5		
	Resistant	mm V_1v	Segregate	12.5		
	Susceptible	mm vv	Susceptible	6.25	7.8	6

Crosses of Resistant x Resistant Parents

In the previous section of this manuscript, a genotype was proposed for each of the crown rust resistant parents based on the ratios obtained from crosses to a fully susceptible parent. Data from crosses among the resistant varieties should provide supporting evidence for the proposed genotypes of the parents and should give more critical data on the extent to which certain of the genes for resistance were allelomorphic. It should be re-emphasized that in certain crosses the number of F_2 generation plants and the number of F_3 progenies grown from each F_2 may not have been large enough to accurately distinguish between homozygous and heterozygous types.

Critical data from crosses among resistant varieties are the occurrence of homozygous susceptible and progenies segregating for resistance and susceptibility. These segregates clearly prove that the parents had different genes for resistance to crown rust.

Ukraine x Klein 69b, cross # 11

A photograph of the reaction of progenies of the parental plants and of the F_2 segregation is shown in Figure 12.

From the results of crosses with Clinton previously given it was shown that Ukraine carried two dominant duplicate linked factor pairs (MM UU) and Klein 69b carried one dominant factor pair for resistance (KK). If these factors were not alleles or closely linked, susceptible plants should be found in the F_2. The segregation for crown rust reaction of the corrected F_2 data is shown in Table 9. The expected values are based on an assumption that the Ukraine factors are epistatic to the Klein 69b factor. It will be recalled that the cross-over between Ukraine factors M and U was estimated to be 0.23.

The chi square-value computed from Table 9 was 21.2 with a probability with 6 degrees of freedom of less than .01. Since 14.8 of the total chi-square came from one class it may be a better fit than the data indicated.

In the class segregating for Ukraine and Klein 69b types 64.5 percent were expected to be of the genotype Mm Uu KK. Of these it was expected 81.7 percent to be in the coupling phase and segregate in the following generation in the ratio of 85.2 percent Ukraine : 14.8 percent Klein 69b. The 18.3 percent in the repulsion phase were expected to segregate 98.7 percent Ukraine : 1.3 percent Klein 69b. The total segregation of this genotype was expected to be 87.67 percent : 12.37 percent. The segregation for the other two genotypes (35.7 percent) in this class was expected to be 75 percent Ukraine : 25 percent Klein 69b. The class segregation was then expected to be 83.18 percent Ukraine : 16.8 percent Klein 69b or from a total of 68 plants the expected numbers were 56.6 : 11.4 and the observed numbers of 54 : 14 indicated a good fit.

In the portion of the F_3 population segregating Ukraine : Klein 69b : susceptible (genotypes Mm Uu Kk, Mm uu Kk and mm Uu Kk) 64.5 percent were expected to be from F_2 plants with the genotype Uu Mm Kk. Of this genotype 81.7 percent were expected to be in the coupling phase and 18.3 percent in the repulsion phase. Of those in the coupling phase the segregation of 98.7 percent Ukraine : 0.66 percent Klein 69b : 0.66 percent

Figure 12. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant parents.

Left half. Ukraine x Klein 69b, cross # 11. Left to right. Ukraine (5-3); F_2 plants 01, 1, 101 and 401; Klein 69b (1-26).

Right half. Ukraine x Trispernia, cross # 76. Left to right. Ukraine (5-18); F_2 plants 01, 1, 201 and 202; Trispernia (2-12).

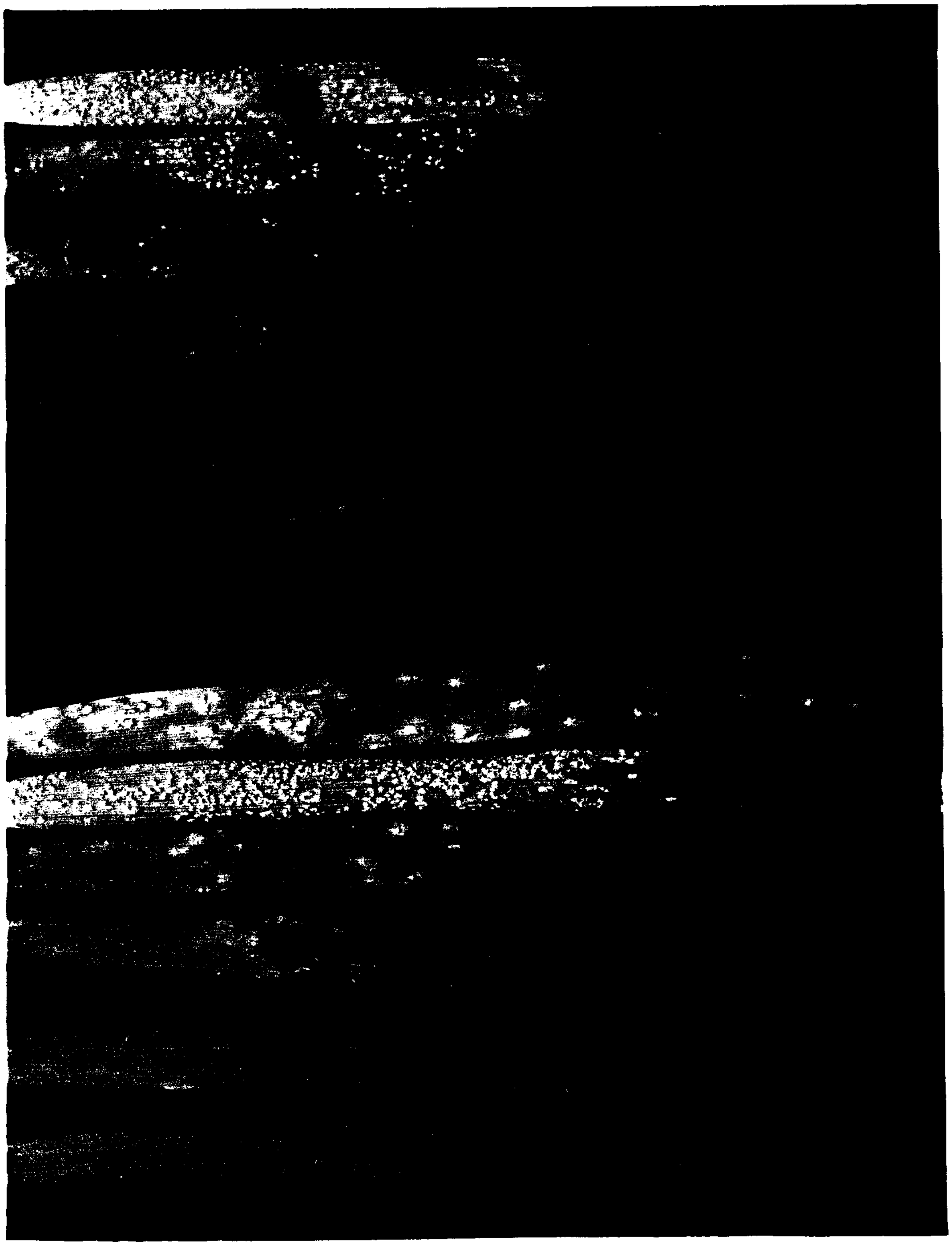


Table 9. Expected and observed frequencies of phenotypic and genotypic classes of corrected F_2 data from a cross of Klein 69b x Ukraine.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs.[1] #
Female Parent 1-26	2 type resistance	$\frac{m\ u\ K}{m\ u\ K}$	Resistant			
Male Parent 5-3	I type resistance	$\frac{M\ U\ k}{M\ U\ k}$	Resistant C.O.= 23% between M and U			
F_1	I type resistance	$\frac{M\ U}{m\ u}$ Kk	Segregate			
F_2	I type resistance	MM ---- / -- UU	I type resistance	35.2	39.5	31
	I type resistance	$\frac{M\ U}{m\ u}$ KK	Segregate Resistant	7.42		
		$\frac{M\ u}{m\ U}$ KK	Segregate Resistant	0.66	14.0	10
		Mm uu KK	Segregate Resistant	2.22		
		mm Uu KK	Segregate Resistant	2.22		
	I type resistance	$\frac{M\ U}{m\ u}$ Kk	Segregate Resistant & Susceptible	14.84		
		$\frac{M\ u}{m\ U}$ Kk	Do.	1.32	28.	27
		Mm uu Kk	Do.	4.44		

[1]Eleven F_2 plants could not be placed definitely in a class because of insufficient progenies. It could be told they belonged in one of the three classes segregating for the Ukraine (immune) type of resistance. They were assigned according to expectation in these classes, i.e. 3 in the class segregating for Ukraine : Klein 69b, 5 in the class segregating for Ukraine : Klein 69b : susceptible, and 3 in the class segregating for Ukraine : susceptible.

Table 9. (continued).

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs.[1] #
		mm Uu Kk	Segregate Resistant & Susceptible	4.44		
	I type resistance	$\frac{M\ U}{m\ u}$ kk	Segregate I type resistance & susceptible	7.42	14	15
		$\frac{M\ u}{m\ U}$ kk	Do.	0.66		
		Mm uu kk	Do.	2.22		
		mm Uu kk	Do.	2.22		
	2 type resistance	mm uu KK	2 type resistance	3.71	4.2	8
	2 type resistance	mm uu Kk	Segregate 2 type resistance & susceptible	7.42	8.3	9
	Susceptible	mm uu kk	Susceptible	3.71	4.2	12

[1]Eleven F_2 plants could not be placed definitely in a class because of insufficient progenies. It could be told they belonged in one of the three classes segregating for the Ukraine (immune) type of resistance. They were assigned according to expectation in these classes, i.e. 3 in the class segregating for Ukraine : Klein 69b, 5 in the class segregating for Ukraine : Klein 69b : susceptible, and 3 in the class segregating for Ukraine : susceptible.

susceptible was expected. The expectation of this genotype was then 87.77 percent : 9.21 percent : 3.15 percent. In the other two genotypes (35.46 percent) the segregation was expected to be 75 percent : 18.8 percent : 6.2 percent. The class segregation was then expected to be 81.7 percent Ukraine : 13.8 percent Klein 69b : 4.6 percent susceptible or from a total of 394 F_3 plants the expected numbers were 321.8 : 54.5 : 18.2 while the observed numbers were 275 : 55 : 64. The observed did not agree with the expected.

In the class segregating for Ukraine : susceptible a 3 : 1 ratio was expected. From a total of 180 F_3 seedlings the observed numbers were 71 : 109 where the expected were 135 : 45. The observed does not fit the expected. The Klein 69 b factor was only partially dominant and this led to difficulty in classification. In some classes the data fit a two factor hypothesis better than the three factor hypothesis. With limited data it was difficult to distinguish between the two hypotheses on the basis of one cross.

<u>Ukraine x Trispernia, cross # 76</u>

This cross involves two resistant varieties, Ukraine having the immune type reaction and Trispernia having a 2 type reaction. A photograph of progenies of the actual parents and the F_2 segregation is shown in Figure 12. No fully susceptible plants were observed in either the F_2 or F_3 generations therefore Trispernia carried at least one factor pair for resistance which was allelic (M_2M_2) to one of the duplicate linked factor pairs from Ukraine (MM UU).

Table 10. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from the cross Ukraine x Trispernia.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 5-18	Resistant I type	$\frac{M\ U}{M\ U}$ 23% C.O.	Resistant			
Male Parent 2-12	Resistant 2 type	M_2M_2 (uu)[1]	Resistant			
F_1	Resistant I type	MM_2 Uu	Segregate			
F_2	Resistant I type	MM --	Resistant I type	17.6	40.8	44
	Do.	-- UU	Do.	17.6		
	Do.	$\frac{M\ U}{M_2u}$	Segregate for I & 2 type resistance	29.8	58.0	55
	Do.	$\frac{M\ u}{M_2U}$	Do.	2.6		
	Do.	$\frac{M\ u}{M_2u}$	Do.	8.8		
	Do.	$\frac{M_2U}{M_2u}$	Do.	8.8		
	Resistant 2 type	$\frac{M_2u}{M_2u}$	Resistant 2 type	14.8	17.2	17

[1]It cannot be determined from this cross if the allel to the U factor from the Trispernia parent is a recessive or a resistant allel of a lower type. It is designated as recessive only as a matter of convenience.

Assuming the Ukraine factors were epistatic and/or dominant to the Trispernia factor the expected ratios were the same as for the cross of Clinton x Ukraine as shown in Table 10 for this cross. On basis of the corrected F_2 data the observed was 44 breeding true Ukraine, 55 segregating Ukraine and Trispernia, and 17 breeding true Trispernia where the expected was 40.8 : 58.0 : 17.2. This was a satisfactory fit.

On the basis of the segregating portion of the population a ratio of 82.3 percent Ukraine : 17.6 percent Trispernia was expected or from a total of 860 F_3 plants the expected was 707.8 : 151.6 and the observed was 677 : 183. A chi square value of 7.70 was obtained having one degree of freedom and a probability of less than .01.

Ukraine x Victoria, cross # 30

This cross was between two resistant varieties, Ukraine (immune) and Victoria, with its distinct type of resistance which is completely linked with susceptibility to H. victoriae. A photograph of progenies of the actual parents and the F_2 segregation for reaction to crown rust is shown in Figure 13.

On the basis of the data from this cross it was assumed that the two dominant linked factor pairs from Ukraine (MM UU) were epistatic and independent to a single dominant factor pair from Victoria (VV). The corrected F_2 data for this cross are given in Table 11.

It is evident from Table 11 that the observed data fit the expected on the above assumed gene action except in the case of the class breeding true for the Victoria type of reaction. The deviation of this class was large enough to give a poor fit according to the chi square test. The reason for such a large deviation in this one class was not evident.

In the segregating portion of the population the expected ratios were the same as those calculated for the previous cross of Ukraine x Klein 69b.

In the portion segregating for Ukraine : Victoria a ratio of 83.2 Ukraine : 16.8 Victoria was expected or from a total of 143 plants the expected numbers were 118.9 : 24.1. The observed numbers wer 96 : 47. This was not a satisfactory fit.

In the portion segregating for Ukraine : Victoria : susceptible a ratio of 81.7 Ukraine : 13.8 Victoria : 4.6 susceptible was expected or from a total of 131 plants the expected was 107.1 : 18.1 : 6.0. The observed was 79 : 35 : 17. Again this was not a satisfactory fit.

In the portion segregating for Ukraine : susceptible a ratio of 83.2 : 16.8 was expected or for a total of 89 plants the expected numbers were 74.0 : 15.0. The observed was 62:27 which was not a satisfactory fit.

In the portion segregating for Victoria : susceptible a ratio of 3 : 1 was expected or from a total of 105 plants the expected numbers were 78.8 : 26.2. The observed numbers were 81 : 24 which is a satisfactory fit.

In this cross it was possible to recognize a certain genotype but the progeny test was not large enough to adequately represent that genotype.

Figure 13. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant parents.

Left half. Ukraine x Victoria, cross # 30. Left to right. Ukraine (5-24); F_2 plants 01, 1 V401, V402, 401; Victoria (3-11).

Right half. Ukraine x Santa Fe, cross # 39. Left to right. Ukraine (5-3); F_2 plants 01, 1 and 101; Santa Fe (4-11).

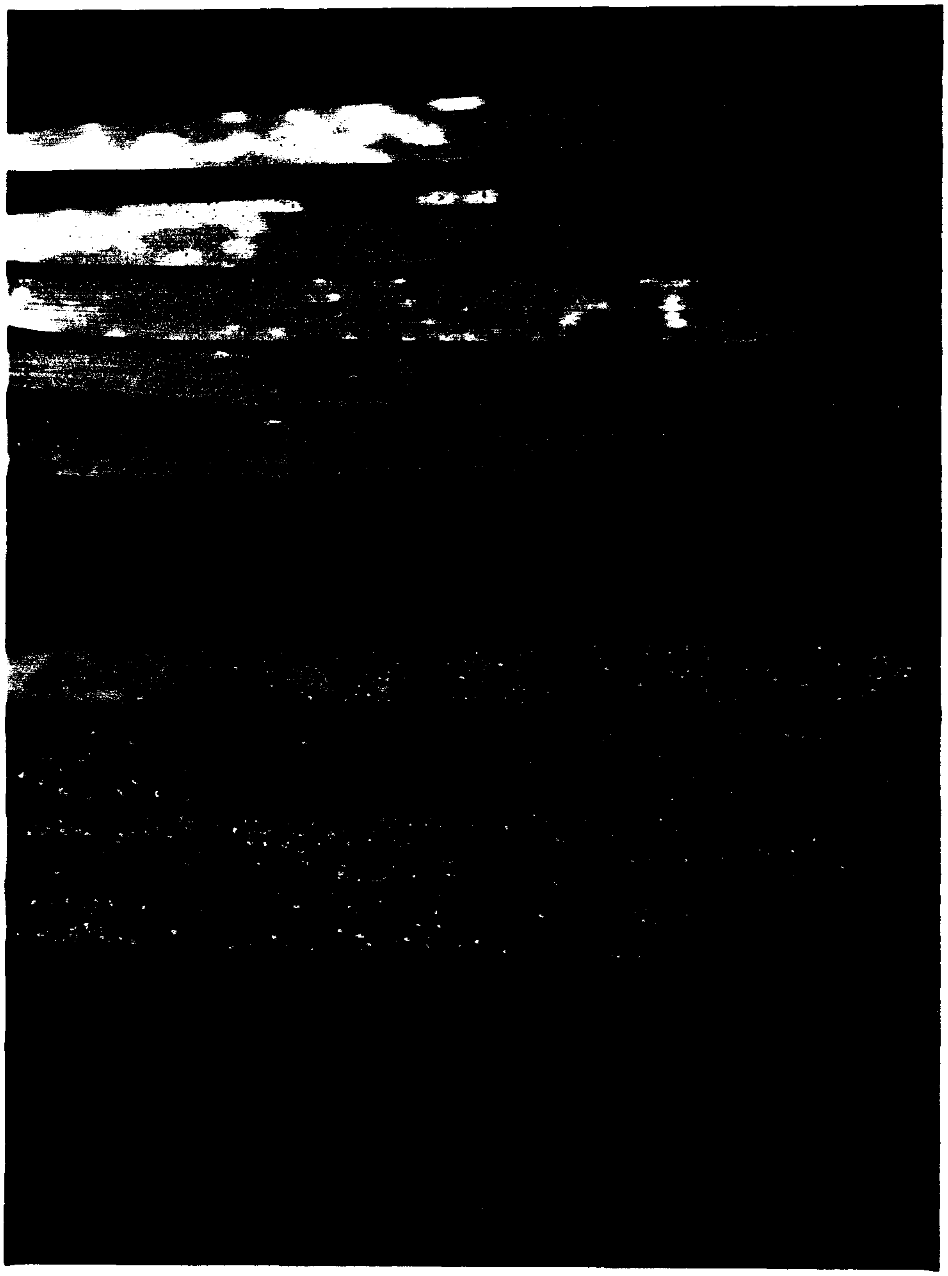


Table 11. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data (both rust reaction and H. victoriae reaction) for a cross of Ukraine x Victoria. Susceptibility to H. victoriae is a pleotropic effect of the gene for crown rust resistance from Victoria.

Generation	Phenotype: Crown rust	Phenotype: H. victoriae	Genotype	Breeding behavior: Crown rust	Breeding behavior: H. victoriae	Exp. %	Exp. #	Obs. #
Female Parent 5-24	Immune	Resistant	$\frac{M\ U}{M\ U}$ vv	Immune	Resistant	23% C.O. between M and U		
Male Parent 3-11	Victoria type	Susceptible	$\frac{m\ u}{m\ u}$ VV	Victoria type	Susceptible			
F_1	Immune	Susceptible	$\frac{M\ U}{m\ u}$ Vv	Segregate	Segregate			
F_2	Immune	Susceptible	MM -- VV	Immune	Susceptible	8.81	7.4	10
	Do.	Do.	-- UU VV	Do.	Do.			
	Do.	Do.	MM -- Vv	Do.	Segregate	17.62	14.8	10
	Do.	Do.	-- UU Vv	Do.	Do.			
	Do.	Resistant	MM -- vv	Do.	Resistant	8.81	7.4	7
	Do.	Do.	-- UU vv	Do.	Do.			
	Do.	Susceptible	Mm Uu VV	Segregate parental types	Susceptible	12.52	10.5	11
	Do.	Do.	Mm uu VV	Do.	Do.			
	Do.	Do.	mm Uu VV	Do.	Do.			

Table 11. (continued).

Generation	Phenotype		Genotype	Breeding behavior		Exp.	Exp.	Obs.
	Crown rust	H. victoriae		Crown rust	H. victoriae	%	#	#
	Immune	Susceptible	Mm Uu Vv	Segregate parental types and susceptible	Segregate	25.04	21	13
	Do.	Do.	Mm uu Vv	Do.	Do.			
	Do.	Do.	mm Uu Vv	Do.	Do.			
	Do.	Resistant	Mm Uu vv	Segregate immune and susceptible	Resistant	12.52	10.5	9
	Do.	Do.	Mm uu vv	Do.	Do.			
	Do.	Do.	mm Uu vv	Do.	Do.			
	Victoria type	Susceptible	mm uu VV	Victoria type	Susceptible	3.71	3.1	13
	Do.	Do.	mm uu Vv	Segregate Victoria and Susceptible	Segregate	7.42	6.2	6
	Susceptible	Resistant	mm uu vv	Susceptible	Resistant	3.71	3.1	5

Ukraine x Santa Fe, cross # 39

This cross was between two resistant varieties Ukraine (immune) and Santa Fe 0 type rust reaction. A photograph of progenies of the actual parents and the F_2 segregation is shown in Figure 13.

It was assumed that Ukraine and Santa Fe had the genes previously described in their respective crosses with Clinton. No fully susceptible plants were observed in the F_2 or F_3 generations indicating the Santa Fe factor pair was allelic (M_1M_1) to one of the linked Ukraine factor pairs (MM UU). The Ukraine factors were dominant or epistatic to the Santa Fe factor. The expected ratio of the corrected F_2 classes as shown in Table 12 was 35.2 percent breeding true Ukraine, 50 segregating for Ukraine and Santa Fe reaction type and 14.8 percent breeding true Santa Fe. The expected numbers were 52.1 : 74.0 : 21.9 from a total of 148 and the observed was 52 : 70 : 26 which is a very good fit.

In the segregating portion of the population accurate readings could not be made since the Ukraine type is only partially dominant or epistatic to the Santa Fe type.

Ukraine x (Anthony-Bond x Boone), cross # 56

This cross involved the immune reaction of Ukraine with a 2 type reaction of A.-B. x Boone. A photograph of the reaction of progenies of the parental varieties and the F_2 segregation are shown in Figure 14.

No fully susceptible plants were observed in the F_2 or F_3 generations of this cross therefore a factor pair for the A.-B. x Boone type of resistance (M_2M_2) must be closely linked or allelomorphic to one of the two factor pairs (MM UU) from Ukraine. The gene action again was partial

Table 12. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from a cross of Ukraine x Santa Fe.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 5-3	Immune	$\frac{M\ U}{M\ U}$ C.O.= 23%	Immune			
Male Parent 8-11	O type	$\frac{M_1 u}{M_1 u}$	O type			
F_1	Immune	$\frac{M\ U}{M_1 u}$	Segregate			
F_2	Do.	MM --	Immune	17.6	52.1	52
	Do.	-- UU	Do.	17.6		
	Do.	$\frac{M\ U}{M_1 u}$	Segregate parental types	29.8	74.0	70
	Do.	$\frac{M\ u}{M_1 U}$	Do.	2.6		
	Do.	$\frac{M\ u}{M_1 u}$	Do.	8.8		
	Do.	$\frac{M_1 U}{M_1\ u}$	Do.	8.8		
	O type	$\frac{M_1 u}{M_1 u}$	O type	14.8	21.9	26

Figure 14. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in a cross between resistant parents.

Ukraine x (Anthony-Bond x Boone), cross # 56. Left to right. Ukraine (5-2); F_2 plants 01, 1 and 201; Anthony-Bond x Boone (14-4).

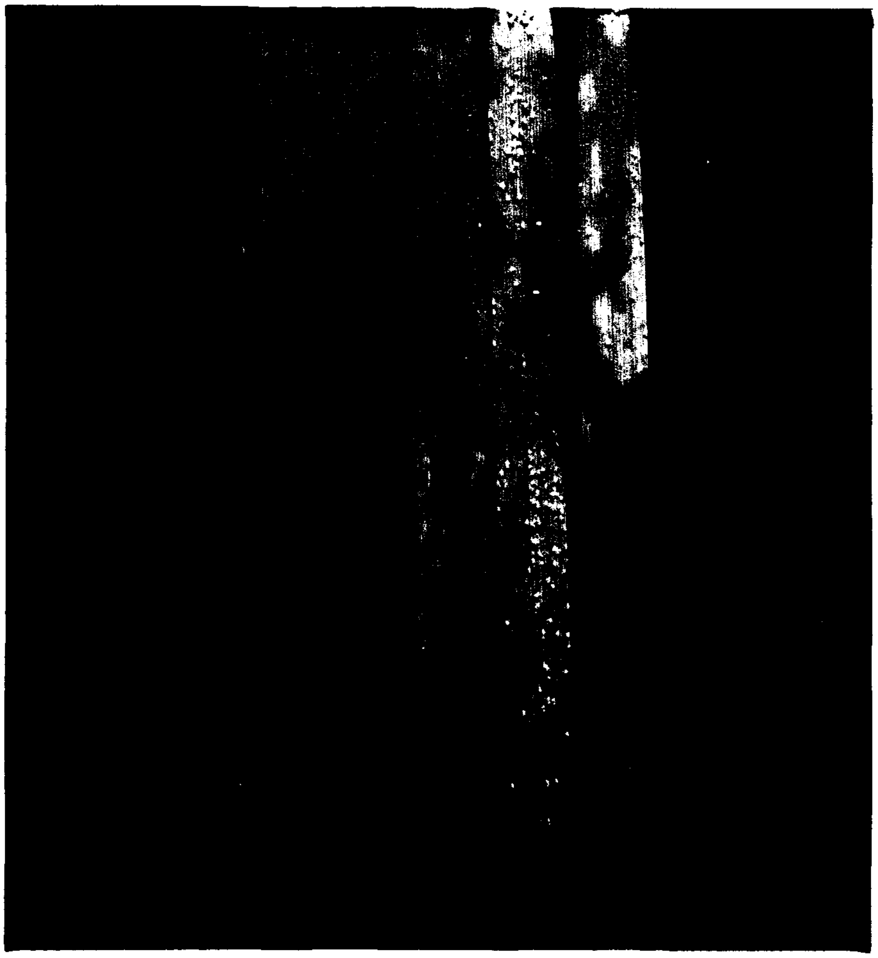


Table 13. Expected and observed frequencies of phenotypic and genotypic classes based on corrected F_2 data from a cross of Ukraine x (Anthony-Bond x Boone).

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 5-2	Immune	$\frac{M\ U}{M\ U}$ C.O.= 23%	Immune			
Male Parent 14-4	2 type	$\frac{M_2u}{M_2u}$	2 type			
F_1	Immune	$\frac{M\ U}{M_2u}$	Segregate			
F_2	Do.	MM --	Immune	17.6	22.2	17
	Do.	-- UU	Do.	17.6		
	Do.	$\frac{M\ U}{M_2u}$	Segregate parental types	29.8	31.5	36
	Do.	$\frac{M\ u}{M_2U}$	Do.	2.6		
	Do.	$\frac{M\ u}{M_2u}$	Do.	8.8		
	Do.	$\frac{M_2U}{M_2u}$	Do.	8.8		
	2 type	$\frac{M_2u}{M_2u}$	2 type	14.8	9.3	10

dominance or epistasis of the linked Ukraine factors.

The ratio of 35.3 percent breeding true Ukraine : 50 segregating for Ukraine and A.-B. x Boone reaction : 14.8 percent breeding true A.-B. x Boone as shown in Table 13 was expected or from a total of 63 plants the expected numbers were 22.2 : 31.5 : 9.3. The observed numbers of 17 : 36 : 10 was a satisfactory fit.

In the segregating portion of the population the expected ratio was 82.2 Ukraine : 17.6 A.-B. x Boone. From a total of 496 F_3 plants the expected numbers were 408.2 : 87.4. The observed numbers were 389 : 107. A chi square value of 5.3 was obtained with one degree of freedom and gave a probability between 0.05 and 0.02.

Victoria x Klein 69b, cross # 69

The data from crosses with Victoria were some of the most critical obtained in this study. The F_2 genotypes could be determined even when the number of progenies tested were small by inoculations with both crown rust and H. victoriae. The crosses of Clinton and Ukraine with Victoria have been discussed previously. The crosses of Trispernia and Santa Fe with Victoria were not available for study.

The data from crosses of Victoria and Klein 69b with Clinton, previously presented, showed the resistance of each of these two varieties was conditioned by a single factor pair. Since the types of resistance were not the same it was assumed that their genes for resistance were different and independent. The reactions of the parental varieties and the F_2 segregations are shown in Figure 15. The F_2 data suggested a two dominant factor hypothesis in which the Victoria factor was epistatic to the Klein 69b factor. The observed and expected numbers on this assumption are shown in Table 14.

The corrected F_2 observed data did not agree well with the expected. The number of F_3 plants in the progeny test may have been too small to identify correctly the F_2 genotype. Under the assumed hypothesis the Victoria gene with its distinctive reaction type would be recovered either in the homozygous or heterozygous condition in 75 percent of the F_2 population. From a total of 78 plants the expected numbers were 58.5 : 19.5 while the observed numbers were 59 : 19. This was a satisfactory fit.

In the portion of the F_2 population that segregated in the F_3 for the Victoria type reaction, 3 Victoria type to 1 other type was expected. The observed was 190 Victoria types : 65 other types and the expected was 191.2 Victoria types : 63.8 other types, an excellent agreement with a 3 : 1 ratio. The observed number of resistant vs. susceptible in the segregating portion of the population giving susceptible plants was 138 resistant : 32 susceptible where the expected numbers were 153 : 17 according to the ratio of 9 : 1. A chi square value of 14.71 with a probability of less than 0.01 was obtained. There was a considerable excess of susceptible plants. While the rust classification is certainly not an absolute one, a better fit than this was expected. The explanation lies in the class that should be segregating 15 resistant to 1 susceptible. Due to inadequate F_3 numbers this class could not be recognized with the expected frequency and even when it could be recognized the ratio of susceptible to resistant plants was much higher than expected. Partial dominance of the heterozygous types may have also resulted in

Figure 15. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses between resistant varieties.

Left half. Victoria x Klein 69b, cross #69. Left to right. Female parent Victoria (3-5); F_2 segregation plants V101, V401 and 401; male parent Klein 69b.

Right half. Victoria x (Anthony-Bond x Boone), cross #35. Left to right. Female parent Victoria (3-8); F_2 segregation V1, V101, V401, 201 and 301; male parent A.-B. x Boone (14-2).

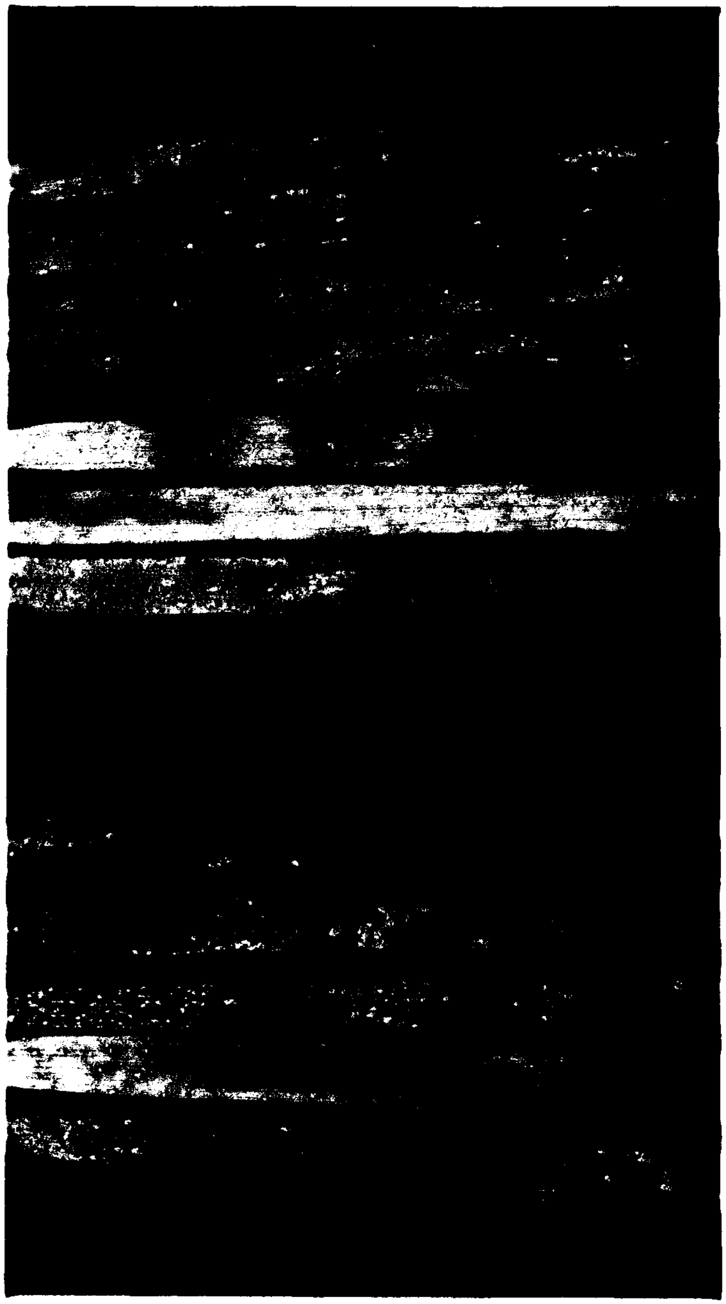


Table 14. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust and *H. victoriae* data from a cross of Klein 69b x Victoria.

Generation	Phenotype: Crown rust	Phenotype: *H. victoriae*	Genotype	Breeding behavior: Crown rust	Breeding behavior: *H. victoriae*	Exp. %	Exp. #	Obs. #
Female Parent 1-30	Resistant 2 type	Resistant	KK vv	Resistant	Resistant			
Male Parent 3-5	Resistant victoria type	Susceptible	kk VV	Resistant	Susceptible			
F_1	Resistant victoria type	Susceptible	Kk Vv	Segregate	Segregate			
F_2	Do.	Do.	KK VV	Resistant	Susceptible	25	19.5	24
	Do.	Do.	Kk VV	Do.	Do.			
	Do.	Do.	kk VV	Do.	Do.			
	Do.	Do.	KK Vv	Segregate Parental types	Segregate Parental types	12.5	9.8	19
	Do.	Do.	Kk Vv	Segregate Parental types & susceptible	Segregate Parental types	25	19.5	7
	Do.	Do.	kk Vv	Segregate Victoria type & susceptible	Segregate	12.5	9.8	9
	Resistant Klein 69b type	Resistant	KK vv	Resistant	Resistant	6.25	4.9	10

Table 14. (Continued).

Generation	Phenotype		Genotype	Breeding behavior		Exp.	Exp.	Obs.
	Crown rust	*H. victoriae*		Crown rust	*H. victoriae*	%	#	#
	Resistant Klein 69b type	Resistant	Kk vv	Segregate Klein 69b type & susceptible	Resistant	12.5	9.8	5
	Susceptible	Resistant	kk vv	Susceptible	Resistant	6.25	4.9	4

misclassification.

Victoria x (Anthony-Bond x Boone), cross # 35

This cross was between two resistant varieties. A photograph of the parental plants and of the segregation in the F_2 is shown in Figure 15.

The progeny test indicated that the corrected F_2 population could be grouped into three classes: (1) one which bred true for the dominant Victoria type, (2) one which segregated for the Victoria and A.-B. x Boone type or, (3) one which bred true for the A.-B. x Boone type as shown in Table 15. The observed numbers were 30 : 46 : 29 and the expected numbers were 26.25 : 52.5 : 26.25. A chi square value of 1.63 with a probability between 0.50 and 0.30 indicated a satisfactory fit.

In the segregating portion of the population where 3 Victoria type rust reaction to 1 A.-B. x Boone type was expected or 425.25 : 141.75 the observed numbers were 442 : 125. A chi square of 2.62 with one degree of freedom and a probability of 0.10 was obtained which indicated a satisfactory fit.

From the cross of Ukraine x (A.-B. x Boone) it was shown that A.-B . x Boone carried a factor for resistance which was allelic to a Ukraine factor. In the cross of Ukraine x Victoria it was shown that the Victoria factor was independent of the Ukraine factor. A.-B. x Boone must carry at least two independent factors for resistance, one being allelic to one of the Ukraine linked factors and the other being allelic to the Victoria factor.

Table 15. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust and *H. victoriae* data from a cross of Victoria x (Anthony-Bond x Boone).

	Phenotype			Breeding behavior				
Generation	Crown rust	*H. victoriae*	Genotype	Crown rust	*H. victoriae*	Exp. %	Exp. #	Obs. #
Female Parent 3-8	Victoria type	Susceptible	VV	Resistant	Susceptible			
Male Parent 14-2	2 type	Resistant	V_1V_1	Resistant	Resistant			
F_1	Victoria type	Susceptible	VV_1	Segregate	Segregate			
F_2	Victoria type	Susceptible	VV	Resistant Victoria type	Susceptible	25	26.2	30
	Do.	Do.	VV_1	Segregate Parental types	Segregate	50	52.5	46
	2 type	Resistant	V_1V_1	Resistant 2 type	Resistant	25	26.2	29

Victoria x Landhafer, cross # 33

The resistance in each of these parents was assumed to be due to a single factor pair based on the results from crosses with Clinton. As in the previous cross, the two parental varieties differed in reaction type and therefore their genotype for resistance might be assumed to be different. The F_2 data suggested that the Landhafer factor was epistatic to the Victoria factor and both were dominant. The F_2 segregation is shown in Figure 16.

In this cross it was possible to identify all genotypes according to their reaction to crown rust and to *H. victoriae*. The observed and expected numbers for the various genotypes are shown in Table 16.

The observed data shown in Table 16 did not agree with the expected. In a test of Landhafer vs. other types where a 3 : 1 ratio was expected or 78.75 : 26.25 the observed was 88 : 17. The chi square value of 4.35 with the probability between 0.05 and 0.02 was obtained. This was not as good a fit as was expected.

In a test of Victoria vs. other types where again a 3 : 1 ratio was expected or 78.75 : 26.25 the observed was 71 : 34. A chi square value of 3.05 with the probability between 0.10 and 0.05 was obtained. This was a satisfactory fit. Resistant vs. susceptible were tested and the expected ratio was 15 : 1 or 98.44 : 6.56 and 103 : 2 was observed. The chi square value of 3.38 was obtained with the probability between 0.10 and 0.05. This too was a satisfactory fit.

In the segregating portion of the F_2 progenies the ratio of Landhafer type to other types was tested. The ratio of 3 : 1 was expected or 288.75 : 96.25 and 265 : 120 was observed. A chi square value

Figure 16. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in a cross of resistant varieties Landhafer x Victoria.

Left half. Variation in the portion of the F_2 segregation that gave the Victoria type crown rust reaction. Left to right. F_2 plants V1, V101, V201, V301 and V401.

Right half. Segregation in the non-Victoria portion of the F_2. Left to right. F_2 plants 1, 101, 201, 301 and 401.

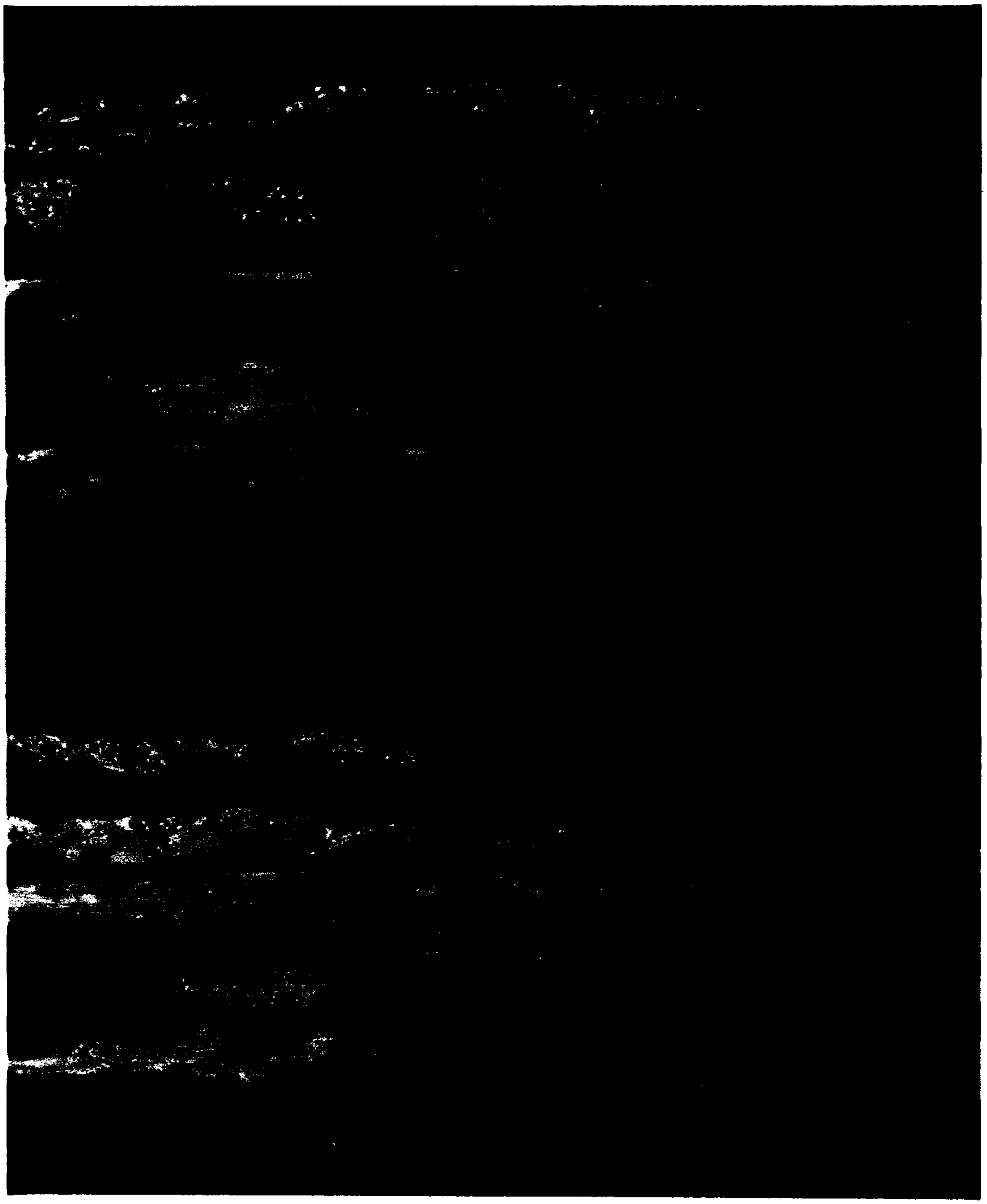


Table 16. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust and *H. victoriae* data from a cross of Landhafer x Victoria.

Generation	Phenotype: Crown rust	Phenotype: *H. victoriae*	Genotype	Breeding behavior: Crown rust	Breeding behavior: *H. victoriae*	Exp. %	Exp. #	Obs. #
Female Parent 6-16	0 type	Resistant	LL vv	Resistant	Resistant			
Male Parent 3-8	Victoria type	Susceptible	ll VV	Resistant	Susceptible			
F_1	0 type	Do.	Ll Vv	Segregate	Segregate			
F_2	0 type	Do.	LL VV	Resistant 0 type	Susceptible	6.25	6.6	29
	Do.	Do.	LL Vv	Do.	Segregate	12.5	13.1	11
	Do.	Resistant	LL vv	Do.	Resistant	6.25	6.6	12
	Do.	Susceptible	Ll VV	Segregate Parental types	Susceptible	12.5	13.1	1
	Do.	Do.	Ll Vv	Segregate Parental types & susceptible	Segregate	25.0	26.2	15
	Do.	Resistant	Ll vv	Segregate 0 type & susceptible	Resistant	12.5	13.1	20
	Victoria type	Susceptible	ll VV	Resistant Victoria type	Susceptible	6.2	6.6	13

Table 16. (Continued).

Generation	Phenotype		Genotype	Breeding behavior		Exp.	Exp.	Obs.
	Crown rust	*H. victoriae*		Crown rust	*H. victoriae*	%	#	#
	Victoria type	Susceptible	11 Vv	Segregate Victoria type & susceptible	Segregate	12.5	13.1	2
	Susceptible	Resistant	11 vv	Susceptible	Resistant	6.25	6.6	2

of 6.83 with a probability of less than 0.01 was obtained. This was not a satisfactory fit.

In the segregating portion of the F_2 progenies the Victoria types vs. others were tested where the ratio of 3 : 5 was expected or 59.25 : 98.75. The observed was 79 : 79. This was not a satisfactory fit.

Progenies segregating Landhafer vs. susceptible gave 192 : 53 where the expected was 183.75 : 61.25. A chi square value of 1.63 with the probability of 0.20 was obtained indicating a satisfactory fit. Progenies segregating for Victoria and susceptibles gave 15 : 3 where 13.5 : 4.5 were expected and was a satisfactory fit.

As in the previous cross the poor agreement was in the group segregating for Landhafer, Victoria, and susceptible types. Here where the numbers 98.2 : 24.6 : 8.2 were expected those observed were 65 : 63 : 3. The progenies numbers were not sufficient to correctly identify or represent this genotype.

<u>Klein 69b x Landhafer, cross # 14</u>

The cross between these two resistant varieties involved a single dominant factor pair from Klein 69b and a single dominant factor pair from Landhafer. The data suggested that the Landhafer factor was epistatic to and independent of the Klein 69b factor. The reaction of the actual parents and of the F_2 segregation is shown in Figure 17.

The expected and observed numbers computed according to the above assumptions are shown in Table 17. The corrected F_2 data could not be assigned exact genotypes but when assigned to the 3 groups as shown in Table 17 a good fit was obtained.

Figure 17. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses of resistant varieties.

Left half. Klein 69b x Landhafer, cross # 14. Left to right. Male parent Landhafer (6-2); F_2 segregation plants 1, 201 and 401; female parent Klein 69b (1-17).

Right half. Trispernia x Landhafer, cross # 27. Left to right. F_2 segregation plants 1, 101, 201, 301 and 401.

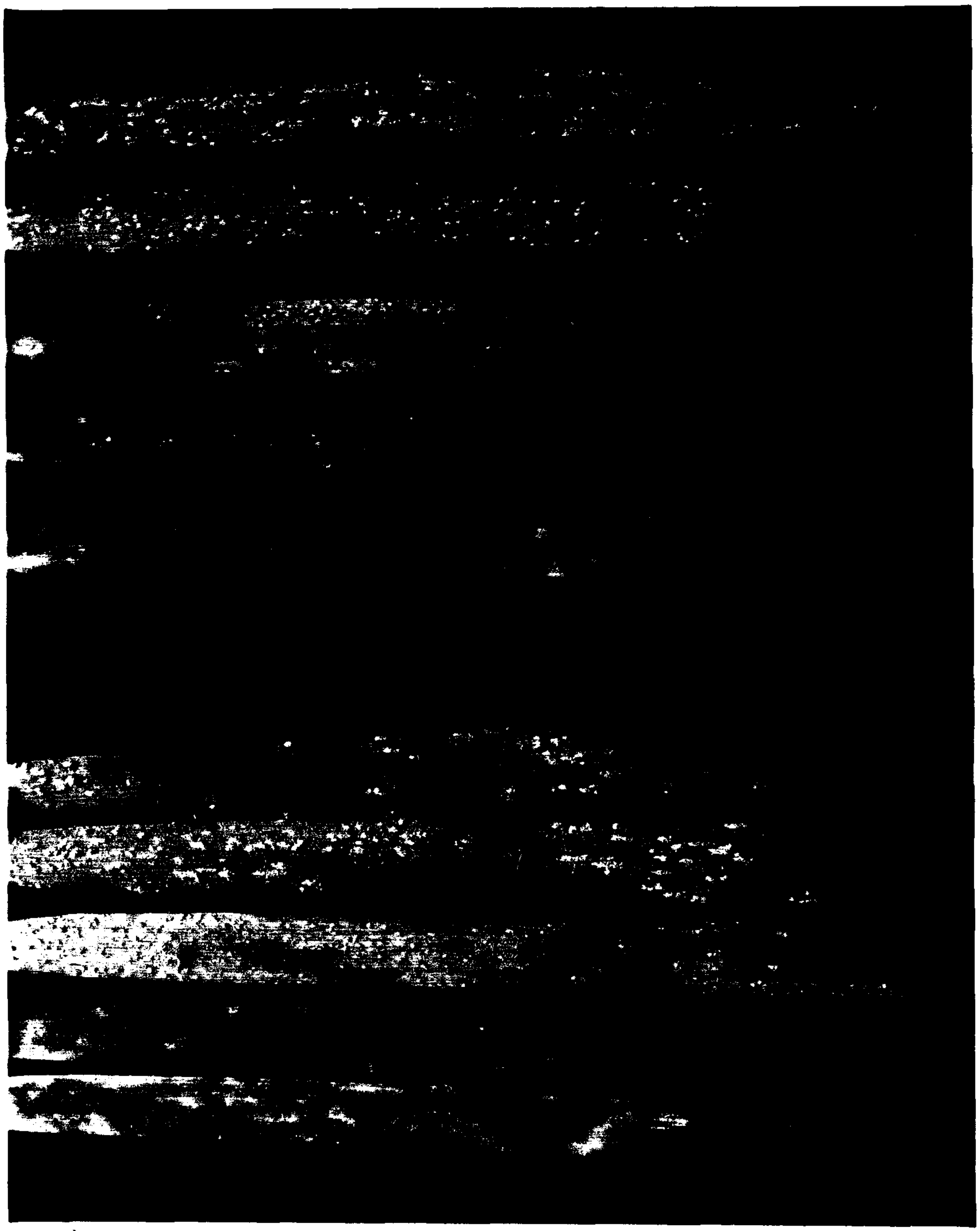


Table 17. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Klein 69b x Landhafer.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 1-17	Resistant	ll KK	Resistant			
Male Parent 6-2	Resistant 0 type	LL kk	Resistant			
F_1	Resistant 0 type	Ll Kk	Segregate			
F_2	Resistant 0 type	LL KK	Resistant 0 type	25	9.2	9
	Do.	LL Kk	Do.			
	Do.	LL kk	Do.			
	Resistant 0 type	Ll Kk	Segregate Parental types & susceptible	68.75	25.4	27
	Do.	Ll kk	Segregate 0 type & susceptible			
	Resistant Klein 69b type	ll KK	Resistant Klein 69b type			
	Do.	ll Kk	Segregate Klein 69 b and susceptible			
	Susceptible	ll kk	Susceptible	6.25	2.3	1

The Landhafer factor was only partially dominant and only when homozygous did it give the 0 type reaction. The data indicated an interaction of the Landhafer and Klein 69b factors when the Landhafer factor was heterozygous. When the Landhafer factor was heterozygous and the Klein 69b factor homozygous a 0 reaction was obtained. When both were heterozygous an intermediate reaction was obtained. Data observed from the Landhafer segregating portion of the population fit the expected very well. The Klein 69b factor was only partially dominant to its allel which made an accurate classification of the portion segregating for Klein 69b and susceptible impossible.

Trispernia x Landhafer, cross # 27

The cross between these two resistant varieties involved a partially dominant and partially epistatic factor from the Landhafer parent which was independent of the partially dominant factor from the Trispernia parent. A photograph of the F_2 segregation is shown in Figure 17.

The expected and observed numbers of groups of genotypes in this cross are shown in Table 18. With the type of gene action indicated above and the limited numbers in the progeny tests it was not possible to correct the genotypes from their breeding behavior. It can be seen from Table 18 that the observed data agrees well with the expected when grouped in the manner described.

Landhafer x Santa Fe, cross # 88

This cross was of more than usual interest since it was between the two major sources of resistance now utilized in several breeding programs.

Table 18. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Trispernia x Landhafer.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 2-23	Resistant 2 type	ll M_2M_2	Resistant			
Male Parent 6-6	Resistant 0 type	LL mm	Resistant			
F_1	Resistant 0 type	Ll M_2m	Segregate			
F_2	Resistant 0 type	LL M_2M_2	Resistant 0 type	25	24.8	22
	Do.	LL M_2m	Do.			
	Do.	LL mm	Do.			
	Do.	Ll M_2m	Segregate Parental types & susceptible	68.75	68.1	71
	Do.	Ll mm	Segregate 0 type & susceptible			
	Resistant 2 type	ll M_2M_2	Resistant 2 type			
	Do.	ll M_2m	Segregate 2 type & susceptible			
	Susceptible	ll mm	Susceptible	6.25	6.2	6

Figure 18. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in a cross of resistant varieties Landhafer x Santa Fe.

Left to right. Female parent Landhafer (6-23); F_2 segregation plants 1 (immune), 5, 101, 201, 202 and 401; male parent Santa Fe (4-16).

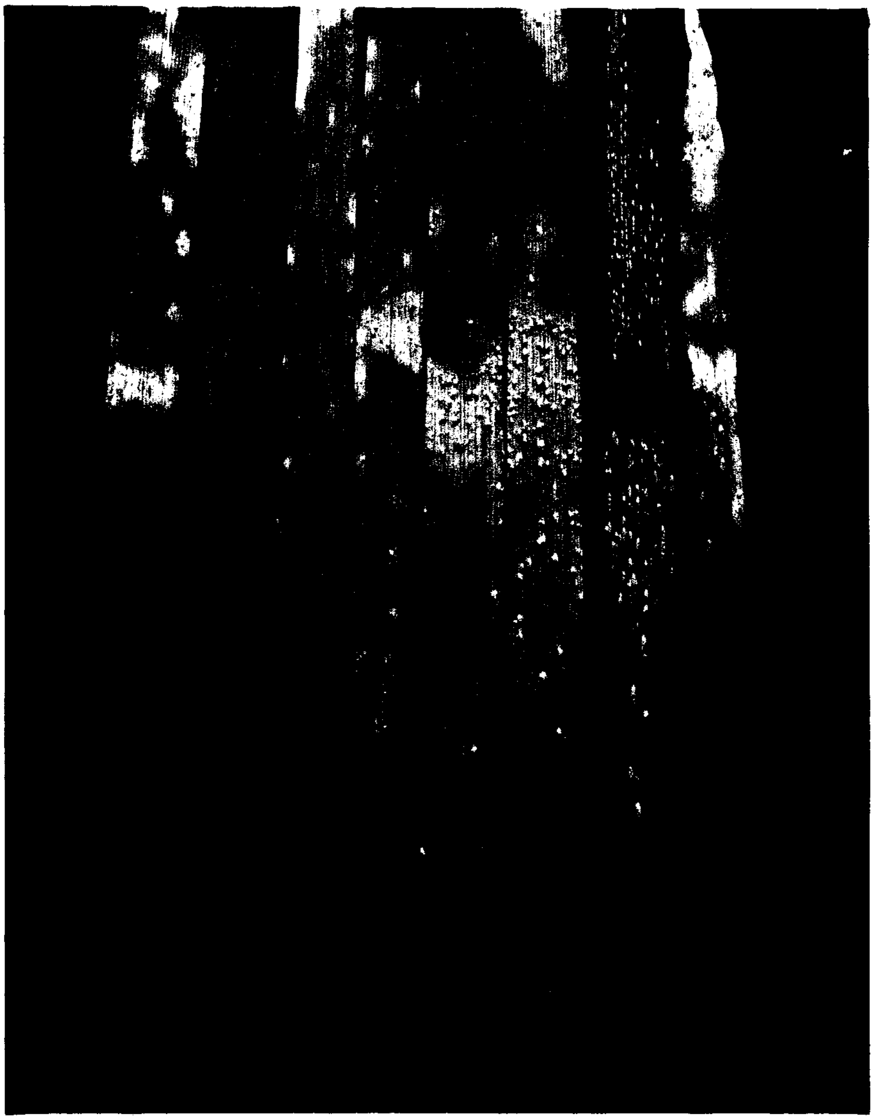


Table 19. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Landhafer x Santa Fe.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 6-23	Resistant O type	LL mm	Resistant			
Male Parent 4-16	Resistant O type	ll M_1M_1	Resistant			
F_1	Resistant O type	Ll M_1m	Segregate			
F_2	Resistant O type	LL M_1M_1	Resistant O type	43.75	49	41
	Do.	LL M_1m	Do.			
	Do.	LL mm	Do.			
	Do.	Ll M_1M_1	Do.			
	Do.	ll M_1M_1	Do.			
	Resistant	Ll M_1m	Segregate Resistant & susceptible	50	56	63
	Do.	Ll mm	Do.			
	Do.	ll M_1m	Do.			
	Susceptible	ll mm	Susceptible	6.25	8	7

On the basis of the genetic analysis from crosses with Clinton this cross involved a partially dominant factor for resistance from Landhafer with an independent partially dominant factor for resistance from Santa Fe. A photograph of the F_2 segregation is shown in Figure 18.

The data presented in Table 19 show a good fit of the observed and expected corrected F_2 genotypes. In the segregating portion of the population a ratio of 7 resistant to 1 susceptible was expected or from a total of 1,062 seedlings the expected numbers were 955.8 : 106.2. The observed numbers were 949 : 113 which was a good fit.

One F_2 plant is shown in Figure 18 which appeared to have an immune rust reaction. From the total F_2 population 2 plants bred true for this type of reaction in the F_3. If this genotype was the double dominant the expected number was 7. This and other F_2 data indicated that immune plants can be obtained by crossing these two varieties, but the genotype of these plants has not yet been confirmed.

Santa Fe x Klein 69b, cross # 9

This cross involved a single partially dominant factor for resistance from Santa Fe which was epistatic to and independent of the partially dominant factor from Klein 69b. A photograph of the F_2 segregation is shown in Figure 19.

The expected and observed numbers of the corrected F_2 data are given in Table 20. It can be seen from the data that the observed numbers agree with the expected. No analysis was made on the segregating portion of the population since partial dominance in this cross made accurate classification in the F_3 impossible without progeny testing.

Figure 19. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses of resistant varieties.

Left half. Santa Fe x Klein 69b, cross #11. Left to right. F_2 segregation plants 2, 106, 206, 316 and 401.

Right half. Trispernia x Santa Fe, cross # 23. Left to right. F_2 segregation plants 1, 101, 201 and 301.

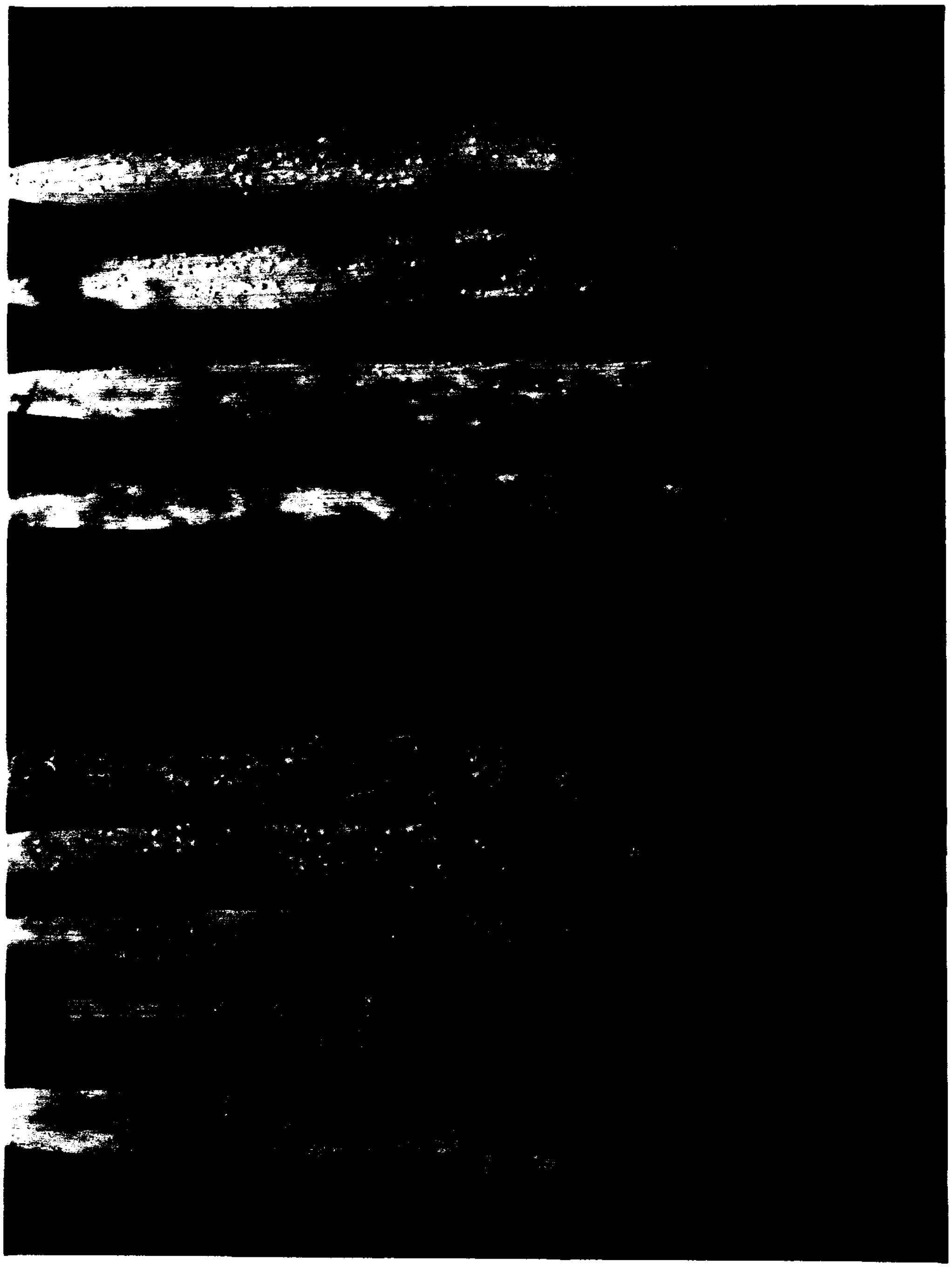


Table 20. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Santa Fe x Klein 69b.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 4-7	Resistant O type	M_1M_1 kk	Resistant			
Male Parent 1-24	Resistant	mm KK	Resistant			
F_1	Resistant O type	M_1m Kk	Segregate			
F_2	Resistant O type	M_1M_1 KK	Resistant O type	25	23	20
	Do.	M_1M_1 Kk	Do.			
	Do.	M_1M_1 kk	Do.			
	Resistant	M_1m KK	Segregate Parental types	68.75	63.2	66
	Do.	M_1m Kk	Segregate Parental types & susceptible			
	Do.	M_1m kk	Segregate O type & susceptible			
	Do.	mm KK	Resistant			
	Do.	mm Kk	Segregate resistant & susceptible			
	Susceptible	mm kk	Susceptible	6.25	5.8	6

Trispernia x Santa Fe, cross # 23

In the cross between these two resistant varieties it was expected that the resistant factors from each variety were alleles or that the factors were linked in the repulsion phase. Since no fully susceptible plants were obtained in the F_2 and only one plant classified as fully susceptible in the F_3 it was assumed that the factors were allelic. The F_2 segregation obtained in this cross is shown in Figure 19.

If the factors were allelic, a 1 : 2 : 1 corrected F_2 ratio was expected for crown rust reaction types, or from a total of 91 plants the expected numbers were 22.75 : 45.5 : 22.75. The observed numbers were 36 : 47 : 8 which was not a satisfactory fit. The observed data appeared to fit a hypothesis such as advanced for the Ukraine crosses, i.e., Santa Fe with two dominant epistatic linked factors for resistance and Trispernia with a factor for resistance which was allelic to one of the two from Santa Fe. Under this hypothesis the expected numbers were 32 breeding true Santa Fe : 45.5 segregating : 13.5 breeding true Trispernia as shown in Table 21. The observed numbers were in agreement with the expected on this basis.

In the segregating portion of the population where a ratio of 82.30 percent Santa Fe types : 17.63 percent Trispernia types was expected from a total of 483 plants, the expected numbers were 398 : 85 and the observed were 349 : 134. The expected ratio was computed on the basis of complete dominance or epistasis of the Santa Fe factors over the Trispernia factor. This probably was not the case since partial dominance or epistasis was the rule in all crosses. It might be expected that the discrepancy would be in classifying too many seedlings in the

Table 21. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Trispernia x Santa Fe.

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 2-22	Resistant 2 type	M_2M_2 uu	Resistant			
Male Parent 4-4	Resistant 0 type	M_1M_1 U_1U_1	Resistant	23% C.O. between M and U		
F_1	Resistant	M_1M_2 U_1u	Segregate			
F_2	Resistant 0 type	M_1M_1 --	Resistant 0 type	35.2	32	36
	Do.	-- U_1U_1	Do.			
	Do.	$\frac{M_1U_1}{M_2u}$	Segregate Parental types	29.8	45.5	47
	Do.	$\frac{M_1u}{M_2U_1}$	Do.	2.6		
	Do.	$\frac{M_1u}{M_2u}$	Do.	8.8		
	Do.	$\frac{M_2U_1}{M_2u}$	Do.	8.8		
	Resistant 2 type	$\frac{M_2u}{M_2u}$	Resistant 2 type	14.8	13.5	8

Trispernia class and too few in the Santa Fe class.

Finding linked duplicate factors in some cases and a single factor in other cases in the Santa Fe variety was not surprising. Santa Fe was not a pure line and while selection had been made for rust resistance in this variety such selection may have failed to differentiate between those plants carrying duplicate linked factors and those carrying but a single factor.

Santa Fe x (Anthony-Bond x Boone), cross # 46

In this cross it was expected the resistant factors would be alleles or linked in the repulsion phase. Since no susceptible plants ~~was~~ were observed in the F_2 and only a very few were classified as susceptible in the F_3 it was assumed the factors were alleles. A photograph of the F_2 segregation is shown in Figure 20 and the summarized data is shown in Table 22.

According to the above hypothesis the corrected F_2 data was expected to be in a ratio of 1 breeding true Santa Fe : 2 segregating : 1 breeding true Anthony-Bond x Boone or from a total of 140 plants the expected numbers were 35 : 70 : 35. The observed numbers were 42 : 64 : 34 which was a satisfactory fit.

Again partial dominance made it impossible to classify the segregating portion of the population correctly.

Klein 69b x Trispernia, cross # 1

In this cross between these two resistant varieties it was expected that segregation would occur for at least two independent factors. A photograph of the F_2 segregation obtained in this cross is shown in

Figure 20. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in a cross of resistant varieties Santa Fe x (Anthony-Bond x Boone).

Left to right. F_2 segregation plants 1, 115, 201 and 323.

Table 22. Observed and expected frequencies of phenotypic and genotypic classes based on corrected F_2 crown rust data from a cross of Santa Fe x (Anthony-Bond x Boone).

Generation	Phenotype	Genotype	Breeding behavior	Exp. %	Exp. #	Obs. #
Female Parent 4-3	Resistant 0 type	M_1M_1	Resistant			
Male Parent 14-6	Resistant 2 type	M_2M_2	Resistant			
F_1	Resistant	M_1M_2	Segregate			
F_2	Resistant 0 type	M_1M_1	Resistant 0 type	25	35	42
	Resistant	M_1M_2	Segregate 0 type & 2 type	50	70	64
	Resistant	M_2M_2	Resistant 2 type	25	35	34

Figure 21.

The data from this cross was not sufficiently complete to place the segregation on a factorial basis. It has been established that Klein 69b had one partially dominant factor pair for resistance. The number of factor pairs contributed throughout by Trispernia was not clear since at least one factor was allelic to one factor from Ukraine and from Santa Fe. The cross of Victoria x Trispernia was not obtained. The cross of Clinton x Trispernia indicated three independent factor pairs. The cross of Landhafer x Trispernia indicated Trispernia had only one factor pair, but the Trispernia parent in this cross was less resistant than other Trispernia parents. This cross indicates Trispernia had two or more factor pairs for resistance which were not allelic to the Klein 69b factor for resistance because susceptible F_2 and F_3 plants were obtained.

Klein 69b x (Anthony-Bond x Boone), cross # 20

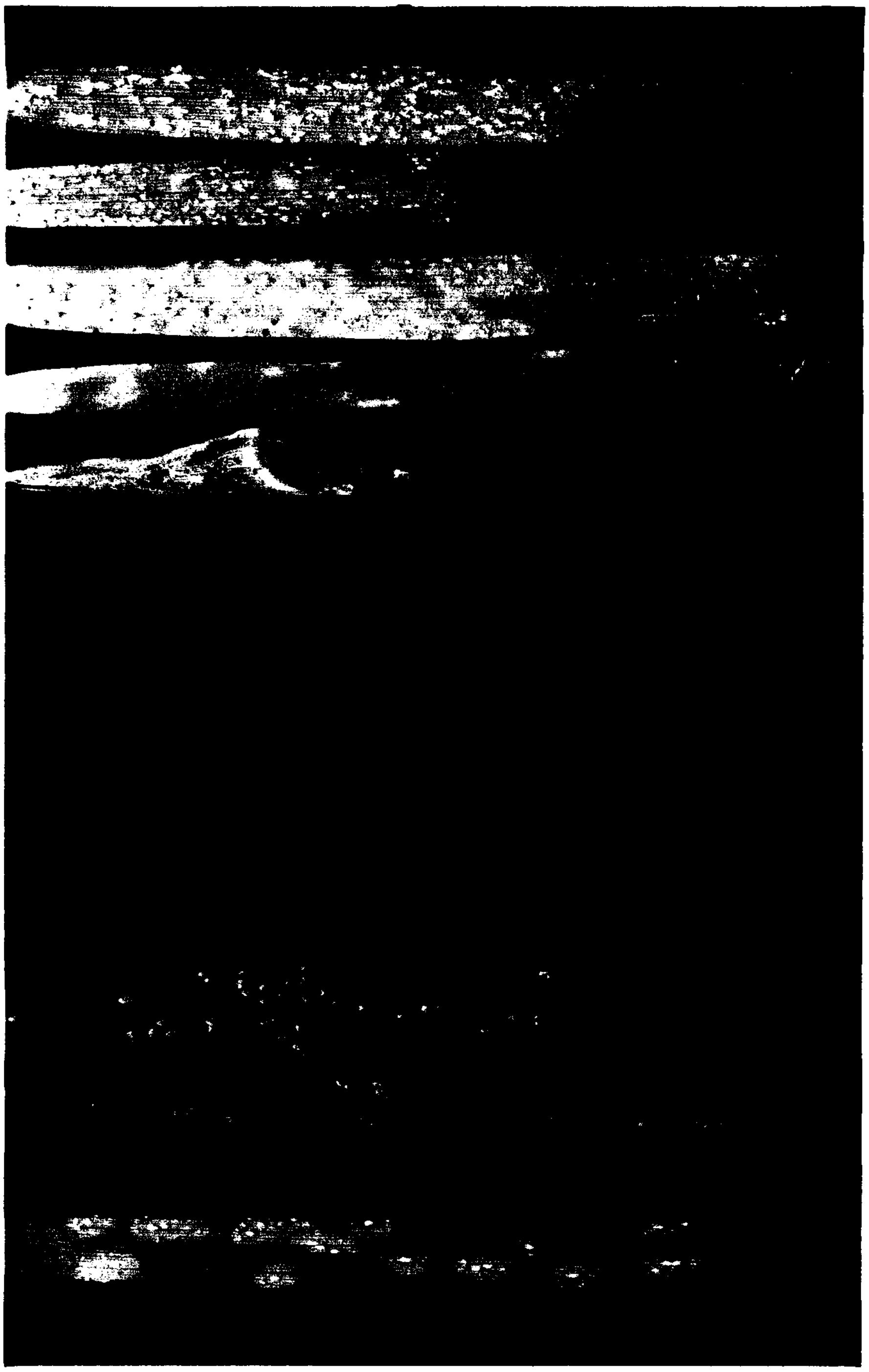
In the cross between these two resistant varieties it was expected segregation would occur for at least three factor pairs. A photograph of the F_2 segregation is shown in Figure 21.

Again the procedure used was insufficient to test such a hypothesis adequately and statistical comparisons were not justified. The data show that segregation does produce susceptible plants in the F_2 and F_3. From 54 F_2 plants progeny tested only one produced an F_3 of all susceptible plants. This indicated, if only weakly, that the hypothesis of three independent factor pairs may be correct.

Figure 21. Segregation obtained in the F_2, for crown rust reaction to a mixture of races, in crosses of resistant varieties.

Left half. Klein 69b x Trispernia, cross # 1. Left to right. F_2 segregation plants 222, 301 and 401.

Right half. Klein 69b x (Anthony-Bond x Boone), cross # 20. Left to right. F_2 segregation plants 1, 104, 218, 301 and 401.



Greenhouse Reaction of F_2 Seedlings to Crown Rust, Race 57

Seedlings grown from remnant F_2 seeds were tested for reaction to race 57. A summary of the data is shown in Table 23.

Due to only partial dominance for resistance as shown in material previously presented, the F_2 data serves only to supplement genetic information rather than providing conclusive genetic ratios.

In four of the crosses the F_2 data did not agree with the expected results on the basis of the hypothesis previously presented. Klein 69b x Clinton had a higher ratio of resistant to susceptible plants than was expected. Difficulty in classification was encountered and this may account for the apparent discrepancies.

Two susceptible F_2 plants were observed from a cross of Ukraine x Santa Fe. The occurrence of these is discussed in the next section.

Plants classified as susceptible were observed in the cross Victoria x (Anthony-Bond x Boone). Since no susceptible plants were expected from this cross, the F_2 plants must be progeny tested to verify their genotype before a change is made in the proposed parental genotypes.

The ratio of resistant to susceptible plants was higher than expected in the cross of Trispernia x Landhafer. A progeny test to verify the F_2 genotypes may correct this ratio.

In all other crosses the F_2 data agreed with that expected.

Greenhouse Reaction of the Hybrid Populations to a Strain of Rust to Which Ukraine was Susceptible

The limited amount of F_2 data obtained in 1949 using this isolate

Table 23. Summary of F_2 seedling reaction in the greenhouse to crown rust race 57.

Cross	Number resistant	Number susceptible	Total Number
Resistant x susceptible			
Klein 69b x Clinton	137	28	165
Trispernia x Clinton	270	8	278
Victoria x Clinton	71	22	93
Santa Fe x Clinton	116	33	149
Ukraine x Clinton	133	25	158
Landhafer x Clinton	160	59	219
Resistant x resistant			
Ukraine x Klein 69b	120	4	124
Ukraine x Trispernia	133	0	133
Ukraine x Santa Fe	304	2	304
Victoria x (A.-B. x Boone)	55	6	61
Victoria x Landhafer	100	4	104
Trispernia x Landhafer	366	6	372
Santa Fe x Landhafer	192	11	203
Santa Fe x Klein 69b	76	6	82
Santa Fe x Trispernia	51	0	51
Santa Fe x (A.-B. x Boone)	117	0	117
Klein 69b x Trispernia	78	11	89
Klein 69b x (A.-B. x Boone)	184	6	190

of rust are shown in Table 24. The data are not extensive enough for genetic interpretations, but some information was obtained.

The data shown in Table 24 show that many of the resistant varieties have different genes for resistance because susceptible plants were obtained in the F_2 of crosses between two resistant parents. It also indicated in crosses with Ukraine that susceptibility was partially dominant. An attempt was made to obtain more information concerning this indication.

After crown rust data had been recorded on the F_2 population of the cross Ukraine x Santa Fe (cross # 39) for a mixture of races, the plants were inoculated on the second or third leaf with a mixture of rust types which contained a large proportion of spores which would attack Ukraine. A photograph of the segregation obtained is shown in Figure 22. A summary of the results is shown in Table 25.

The data in Table 25 indicated the Ukraine type of resistance to race 57 is associated with susceptibility to the race which attacks Ukraine. The association was very close but not absolute if the phenotypic reaction was a correct measure of the genotype. This indicated the factor pair conditioning the Santa Fe type of resistance to race 57 may not be allelic to one of the two linked factor pairs for resistance to race 57 from Ukraine, but instead was closely linked to one of the Ukraine factors. If this was the case one crossover type would be expected to be fully susceptible to race 57.

From cross # 40, (which had the same actual parents as cross # 39) 59 F_2 plants were grown of which 28 were inoculated with the mixture of races which did not parasitize Ukraine and 31 were inoculated with a

Figure 22. Segregation obtained in the F_2 generation, for crown rust reaction to a mixture of races some to which Ukraine was susceptible, in a cross between resistant Santa Fe and susceptible Ukraine.

Left to right. F_2 segregation. First leaf. Plant # 1. Resistant to race Ukraine. Was resistant to mixture of races and segregated in the following generation for the Ukraine type and Santa Fe type resistance to race 57. Second leaf. Plant # 111. Resistant to race Ukraine. Was resistant to mixture of races and bred true for Santa Fe type resistance to race 57. Third leaf. Border line between resistant and susceptible to race Ukraine. Was immune to mixture of races and segregated for Ukraine type and Santa Fe type of resistance in the following generation. Fourth leaf. Susceptible to race Ukraine. Was immune to mixture of races and bred true immune in the following generation to race 57.

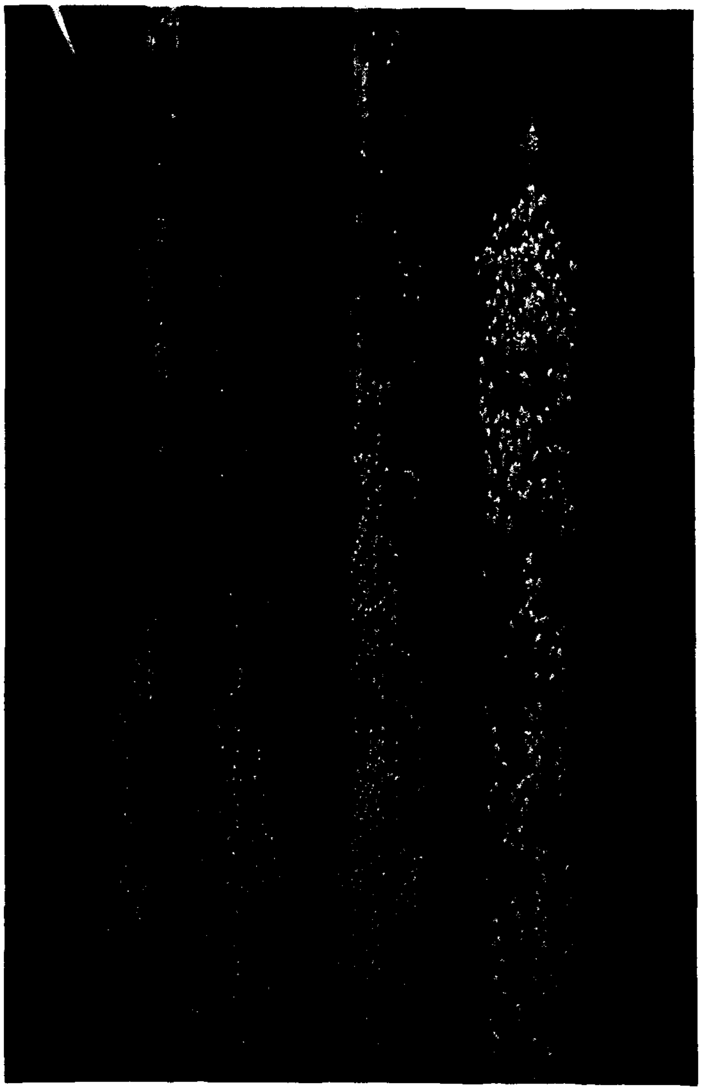


Table 24. Observed numbers of resistant and susceptible F_2 plants to a strain of crown rust to which Ukraine was susceptible.

Parent	Klein 69b	Trispernia	Victoria	Santa Fe	Ukraine	Landhafer	Clinton	A.-B. x Boone
Klein 69b	Mesothetic	7 Res. 3 Sus.	0 Res. 21 Sus.	2 Res. 1 Sus.	20 Res. 87 Sus.	---	4 Res. 57 Sus.	1 Res. 1 Sus.
Trispernia		Resistant	---	1 Res. 1 Sus.	1 Res. 8 Sus.	131 Res. 19 Sus.	3 Res. 30 Sus.	---
Victoria			Resistant	---	---	3 Res. 0 Sus.	27 Res. 9 Sus.	12 Res. 3 Sus.
Santa Fe				Resistant	51 Res. 95 Sus.	---	102 Res. 48 Sus.	111 Res. 9 Sus.
Ukraine					Susceptible	---	0 Res. 189 Sus.	3 Res. 25 Sus.
Landhafer						Resistant	14 Res. 9 Sus.	---
Clinton							Susceptible	---
A.-B. x Boone								Resistant

mixture of races some of which parasitized Ukraine. Progenies of each F_2 plant were divided, part being tested with race 57 and part being tested for reaction to the mixture of races which included some which parasitized Ukraine. The results obtained are shown in Table 26.

Since the mixture of rust strains some of which attacked Ukraine was in storage for several months the viability of the spores was very low and infection of the F_3 seedlings was not complete. Whenever one or more susceptible F_3 seedlings was found it was assumed the F_2 genotype was homozygous or heterozygous for the Ukraine type. The separation of the Ukraine and Santa Fe types for race 57 in the F_3 seedlings also was difficult. Whenever one or more F_3 seedlings showed some pustule formation it was assumed the F_2 genotype was homozygous or heterozygous for the Santa Fe type.

The data in Table 26 also indicated that a relationship was present between the Ukraine type of resistance to race 57 and susceptibility to a strain of rust which attacks the Ukraine parent. Again this relationship was not absolute. More important is the fact that 2 true breeding susceptible plants were observed in this cross. These 2 susceptible plants were the only ones found from a total of 362 F_2 plants tested in the greenhouse and 400 F_2 plants tested in the field. In the F_3 generation no susceptible plants were observed (other than the progenies of the two mentioned) in over 3,000 plants. If the Santa Fe factor is allelic to one of the Ukraine factors the susceptible plants must have resulted from seed mixtures in the F_2 seed supply.

Table 25. Correlated inheritance of two crown rust strains in a cross of Ukraine x Santa Fe, cross # 39.

Race 57 Phenotype	Corrected F_2 observed No.	Uncorrected frequency distribution of F_2 plants with respect to crown rust reaction type when inoculated with race Ukraine. 1 type	2 type	3 type	4 type
Bred true Ukraine type (Immune type)	52	0	2	10	40
Segregated Ukraine and Santa Fe types	70	4	14	41	11
Bred true Santa Fe type (0 type)	26	4	18	3	1

Investigations With *H. victoriae*

The F_2 progenies of the five crosses involving Victoria as one parent were tested for reaction to *H. victoriae*. It was assumed that the dominant factor pair for susceptibility to *H. victoriae* was the same as or completely linked with the Victoria type of crown rust resistance.

Victoria x Clinton, cross # 34

Among the progenies of 125 F_2 plants the observed corrected F_2 data were 34 breeding true susceptible to *H. victoriae*, 64 segregating susceptible and resistant and 27 breeding true resistant. The expected numbers on a single factor hypothesis were 31.25 : 62.50 : 31.25. A chi square value of 0.86 with 2 degrees of freedom gives a probability between 0.50 and 0.30, a satisfactory fit.

Counts were made in only twenty F_3 lines from the segregating portion of the F_2 population. From a total of 305 plants the observed numbers were 216 susceptible : 89 resistant and the expected were 228.75 : 76.25. A chi square value of 2.84 was obtained having one degree of freedom with a probability between 0.10 and 0.05. This was a satisfactory agreement with the assumption of monogenic inheritance of reaction to *H. victoriae* in this cross.

Victoria x Klein 69b, cross # 69

The same segregation for reaction to *H. victoriae* was expected in this cross as was indicated in the cross of Victoria x Clinton. The corrected F_2 observed numbers were 24 : 35 : 19 where the expected were

19.5 : 39 : 19.5. The agreement between the observed and expected was good.

In the segregating portion of the population where 353 plants were tested the observed numbers were 248 susceptible : 105 resistant where the expected numbers were 264.8 : 88.2. A chi square value of 4.25 was obtained having 1 degree of freedom and a probability between 0.05 to 0.02. This was not as good of a fit as was expected.

<u>Victoria x Ukraine, cross # 30</u>

A similar hypothesis of monogenic inheritance of reaction to *H. victoriae* was advanced for this cross. From corrected data on 83 F_2 plants the observed numbers were 33 : 29 : 21 where the expected were 20.8 : 41.5 : 20.8. Here the observed did not agree with the expected. However, with a very limited number of progeny from many F_2 plants it was expected that the deviations would increase the numbers in the class breeding true susceptible and decrease the number in the segregating class.

In the segregating portion of the population the observed numbers were 285 : 80 where 273.8 : 91.2 were expected. A chi square value of 1.85 was obtained with 1 degree of freedom and the probability between 0.20 and 0.10 indicated a satisfactory fit.

<u>Victoria x Landhafer, cross # 33</u>

In this cross where a 1 : 2 : 1 ratio might be expected, the corrected F_2 data showed 43 bred true susceptible, 27 segregated and 34 bred true resistant. The observed segregation did not agree with the expected, even if consideration is made for the small numbers in some of the progenies. In the segregating portion of the population, however, from a total of 264 plants the observed segregation was 196 : 68 where the expected was 198 : 66. This was a satisfactory fit. The F_2 may not have been a good sample of the true genotypic ratio.

Victoria x (Anthony-Bond x Boone), cross # 35

The observed corrected F_2 numbers in this cross were 30 : 46 : 29 where the expected was 26.25 : 52.5 : 26.25 on a single factor basis. A chi square value of 1.63 with two degrees of freedom gave a probability between 0.50 and 0.30. This was a satisfactory fit.

In the segregating portion of the population from a total of 697 plants the observed numbers were 530 : 167 where 522.75 : 174.25 were expected. This also was a satisfactory fit to a single factor hypothesis.

In none of the crosses was there any indication of broken linkage between the Victoria type of crown rust resistance to race 57 and susceptibility to H. victoriae.

Inheritance of Dwarf Plants

The term dwarf often has been used loosely in the literature to describe a condition where the offspring is not as large in size as the parents, without regard to the degree of reduction. It is doubtful if the same principles are involved in the partial reduction of size without loss of vigor or the capacity to reproduce, and in the reduction of size to such a point that the plant never develops past the first or second leaf stage, or tillers profusely and the tillers remain as grassy tufts seldom producing seed.

Dwarf plants of various types were recognized in many of the crosses. It was possible to distinguish only the extreme types in the greenhouse, with certainty, where the plants were grown under variable conditions of crowding, transplanting etc. Only in the cross of Landhafer x Clinton were the dwarf plants sufficiently frequent and recognizable to justify extensive recording of the data.

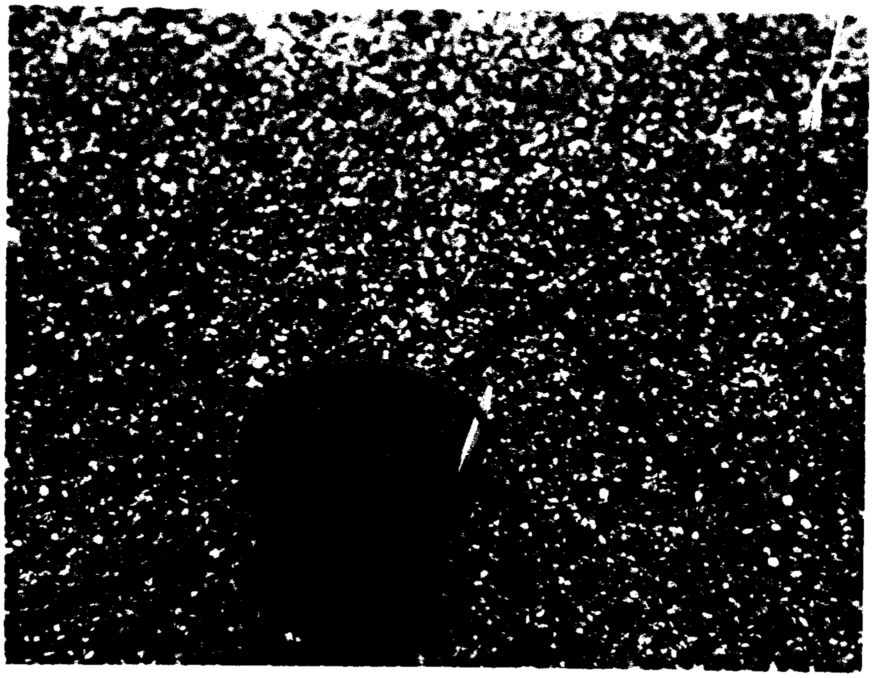
In this cross the dwarf plants were generally of two types. In one of the types the plant failed to develop beyond the first leaf stage. Many of these plants remained alive for several months without further development or growth. The other type produced profuse tillers of short narrow leaves. These plants were quite variable in the amount of growth produced, were much reduced in comparison to the normal plants, but remained alive for several months. Many of them produced short stems with reduced panicles which seldom emerged from the leaf sheath. Such plants rarely produce seed and in this study one dwarf plant produced five seeds.

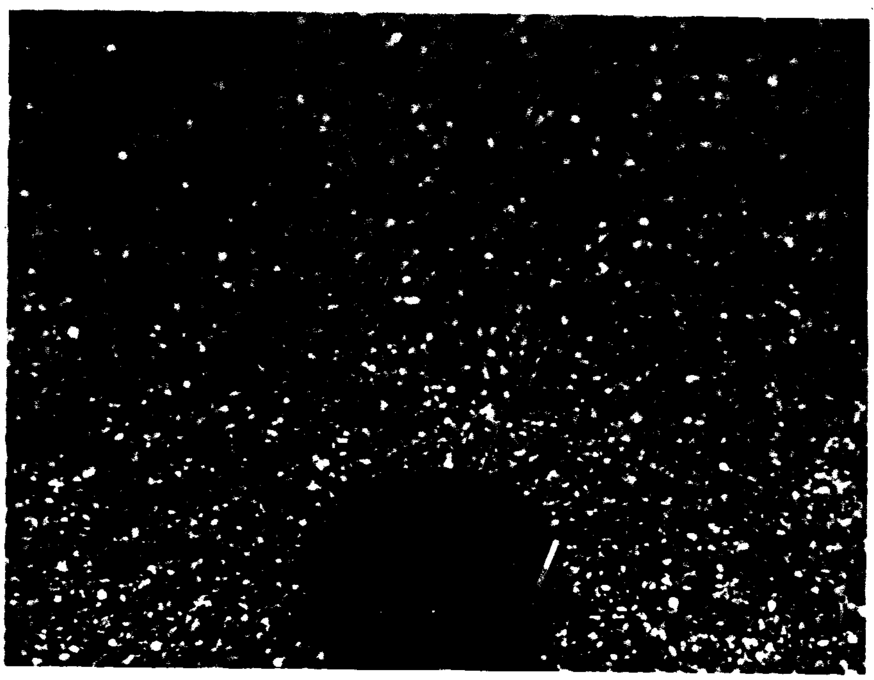
The dwarf plants could be recognized with a fair degree of accuracy in the first leaf stage. No differences were noted in the rate of development of the first leaf between the normal and dwarf plants. Dwarf plants generally were darker green in color and had a thicker leaf. In the later development of dwarfs that tillered, the second and third leaves appeared to arise at the same place as the first leaf with extreme reduction of internode length. Photographs of the two types of dwarfing and normal plants of the same age are shown in Figure 23. A summary of

Figure 23. Dwarf and normal F_2 plants of the same age from a cross of Landhafer x Clinton.

Upper photograph. First leaf dwarf plant on the left and normal plant on the right.

Lower photograph. Tillering type of dwarf plant on the left and a normal plant on the right.





the observed and expected numbers of dwarf and normal plants on the assumption of a 2 complementary factor pair interaction from three F_2 populations of Landhafer x Clinton is shown in Table 27. The genetic explanation, pooled F_2 data and corrected F_2 data for cross # 89 are shown in Table 28.

It was assumed each parent carried a partially dominant complementary factor pair for dwarfing. The assumption of complementary gene action was justified since in many other crosses with each of these parents the dwarf plants of the type described were not observed.

The parental genotypes may be designated as $D_1D_1d_cd_c$ for Landhafer and $d_1d_1D_cD_c$ for Clinton. The F_1 would have the genotype of $D_1d_1D_cd_c$ which would appear normal due to only partial dominance of the dwarf genes. The F_2 phenotypic ratio was expected to be 11 normal : 5 dwarf. It can be seen from data in Tables 27 and 28 the observed data agreed with the expected. On basis of corrected F_2 data the expected ratio was 5 dwarfs (breeding behavior could not be checked as nearly all were lethals) : 7 true breeding normals : 4 normals that segregated giving dwarf and normal plants in the next generation. The expected numbers were 37.2 : 52.1 : 29.7 for cross # 89 and the observed were 47 : 49 : 23. A chi square of 4.3 was obtained having 2 degrees of freedom and a probability of 0.2 to 0.1 which indicated a satisfactory fit.

In the segregating portion ($D_1d_1D_cd_c$) of the F_2 population a phenotypic ratio of 11 normal : 5 dwarf was expected. The expected numbers were 231.7 : 105.3 and the observed numbers were 266 : 71. This was not a satisfactory fit, but absolute classification of seedling plants was not possible.

Table 27. Summary of observed F_2 data for normal and dwarf plants from crosses of Landhafer x Clinton where the parents and F_1's were normal.

Cross No.	Observed No. Normal	Observed No. Dwarf	Expected No. Normal	Expected No. Dwarf	Chi-square	P
89	72	47	81.8	37.2	4.2	.05-.02
90	84	31	79.1	35.9	1.0	.5-.3
91	65	38	70.8	32.2	1.5	.3-.2
Pooled	221	116	231.7	105.3	1.6	.3-.2
Total			3 degrees of freedom		6.7	.1-.05
Interaction			2 degrees of freedom		5.1	.1-.05

Table 28. Observed and expected numbers of normal and dwarf plants in crosses of Landhafer x Clinton.

Generation	Phenotype	Genotype	Breeding behavior	Total F_2 Exp. #	Total F_2 Obs. #	Corrected F_2[1] Exp. #	Corrected F_2[1] Obs. #
Landhafer parent	Normal	$D_1D_1d_cd_c$	Normal				
Clinton parent	Normal	$d_1d_1D_cD_c$	Normal				
F_1	Normal	$D_1d_1D_cd_c$	Segregate				
F_2	Normal	$D_1D_1d_cd_c$	Normal	231.7	221	52.1	49
	Do.	$D_1d_1d_cd_c$	Do.				
	Do.	$d_1d_1D_cD_c$	Do.				
	Do.	$d_1d_1D_cd_c$	Do.				
	Do.	$D_1d_1D_cd_c$	Segregate			29.7	23
	Dwarf	$D_1D_1D_cD_c$	Lethal	105.3	116	37.2	47
	Do.	$D_1d_1D_cD_c$	Do.				
	Do.	$D_1D_1D_cD_c$	Do.				

[1]Data from cross # 89.

Table 29. Test of independence of locus for crown rust reaction and loci for dwarfing in crosses of Landhafer x Clinton where a partially dominant factor pair from Landhafer controls crown rust resistance to race 57 and a partially dominant factor pair from each parent acting complementary controls dwarfing.

Size		Crown rust reaction to race 57 Resistant	Susceptible	Total
Normal	Observed No.	154	59	213
	Expected No.	149.2	63.8	
Dwarf	Observed No.	75	39	114
	Expected No.	79.8	34.2	
Total		229	98	327

Chi-square = 1.5 Probability between 0.3 and 0.2

This hypothesis may also explain the difference between the two types of dwarfs. The dwarfs which never develop beyond the first leaf stage may be of the genotype $D_1D_1D_cD_c$ while the others are $D_1D_1D_cd_c$ or $D_1d_1D_cD_c$.

If this was the case the expected ratio of rosette to first leaf dwarfs would be 4 : 1. Records were kept on the type of dwarfing for cross # 89. From a total of 47 dwarfs the observed number of rosette type dwarfs was 36 and the first leaf dwarfs 11. The expected numbers were 37.6 : 9.4. The agreement between the expected and observed was good.

There was no association between the Landhafer loci for crown rust resistance to race 57 and either loci of the dwarfing factors as shown in Table 29.

Inheritance of Leaf Sheath Pubescence

Segregation for amount of leaf sheath pubescence was observed in all crosses. Some of the parental types are shown in Figures 24, 25, 26 and 27. Although there was considerable variation in the F_2 seedlings they were grouped into four classes; (1) leaf sheath glaborous like the parental types of Clinton, Trispernia and Anthony-Bond x Boone, (2) few leaf sheath hairs like the parent Klein 69b, (3) several leaf sheath hairs like the parent Victoria and some Ukraines, and (4) many leaf sheath hairs like the parents Santa Fe, Landhafer and some Ukraines as shown in Table 30. The class types from the F_2 of a cross of Santa Fe (many) x (Anthony-Bond x Boone) (absent) are shown in Figure 28.

Figure 24. First leaf sheath pubescence of progeny of actual parents.

Left half. Variety Klein 69b. Left to right. Plants 1-17, 1-26 and 1-30.
Right half. Variety Trispernia. Plant 2-12.

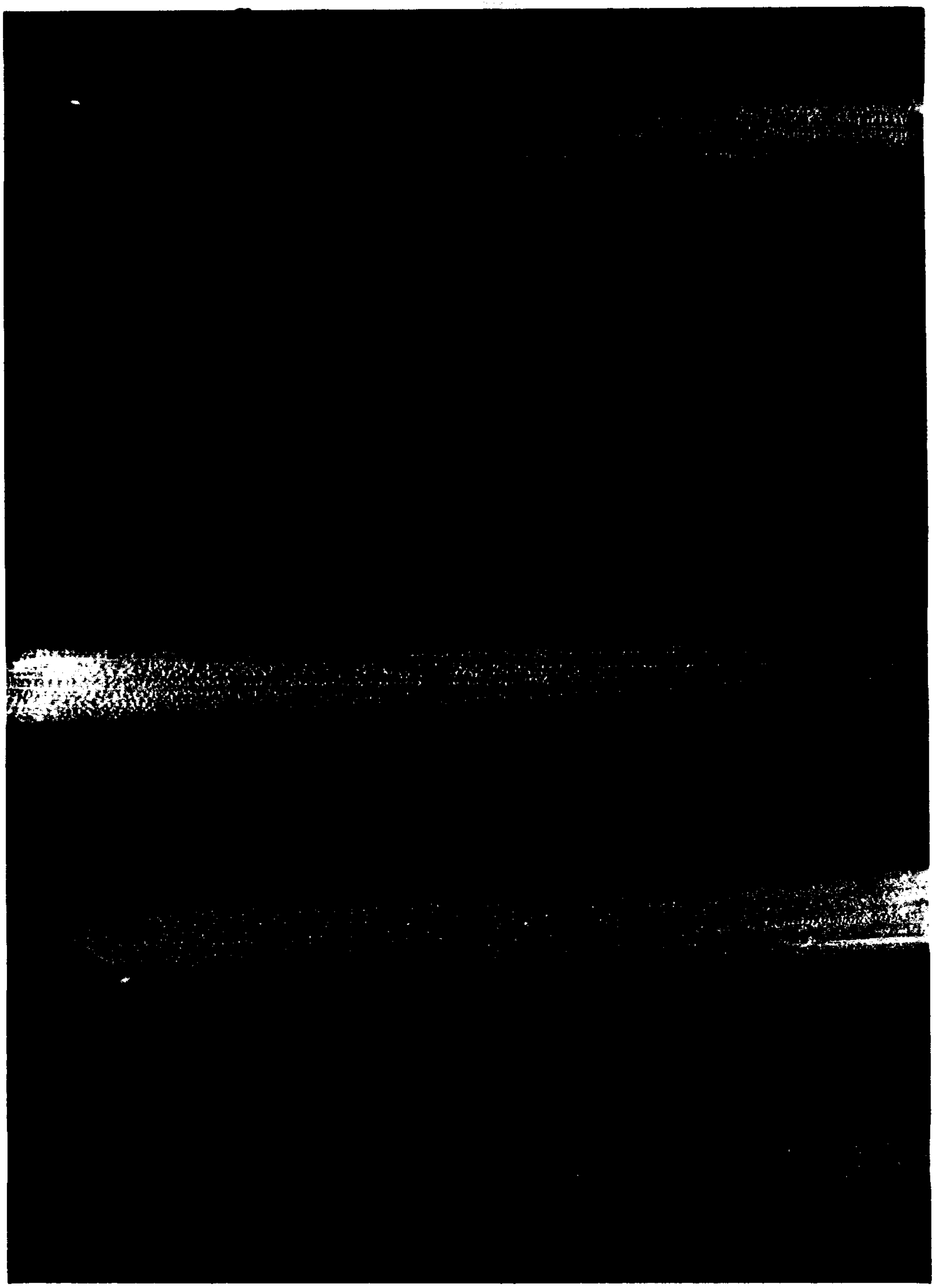


Table 30. F_2 segregation for amount of leaf sheath pubescence in 23 oat crosses.

Cross No.		Absent	Few	Several	Many	Total
	Absent x Absent					
78	Trispernia x Clinton	73	82	-	-	155
164	(A.-B. x Boone)x Clinton	96	33	-	-	129
	Absent x Few					
1	Trispernia x Klein 69b	32	26	20	10	87
18	Clinton x Klein 69b	112	13	-	-	125
20	(A.-B. x Boone)x Klein 69b	63	25	6	1	96
	Absent x Several					
34	Victoria x Clinton	89	40	4	-	133
35	Victoria x(A.-B. x Boone)	31	48	18	12	109
	Absent x Many					
48	(A.-B. x Boone)x Santa Fe	40	17	28	60	145
56	(A.-B. x Boone)x Ukraine	13	11	12	28	64
23	Trispernia x Santa Fe	10	16	19	61	106
76	Trispernia x Ukraine	9	45	34	36	124
27	Trispernia x Landhafer	20	35	41	49	145
46	Clinton x Santa Fe	50	27	22	23	122
55	Clinton x Ukraine	75	56	6	-	137
89	Clinton x Landhafer	75	31	12	-	118

Table 30. (Continued).

Cross No.		Absent	Few	Several	Many	Total
	Few x Several					
69	Klein 69b x Victoria	7	36	26	24	93
	Few x Many					
9	Klein 69b x Santa Fe	24	24	10	48	105
11	Klein 69b x Ukraine	38	39	38	26	141
14	Klein 69b x Landhafer	-	9	11	21	41
	Several x Many					
30	Victoria x Ukraine	1	11	33	53	100
33	Victoria x Landhafer	19	37	34	44	134
	Many x Many					
39	Santa Fe x Ukraine	4	8	32	120	164
88	Santa Fe x Landhafer	-	7	12	103	122

Figure 25. First leaf sheath pubescence of progeny of actual parents.

Left half. Variety Victoria. Left to right. Plants 3-5, 3-8 and 3-11.
Right half. Variety Santa Fe. Left to right. Plants 4-11 and 4-16.

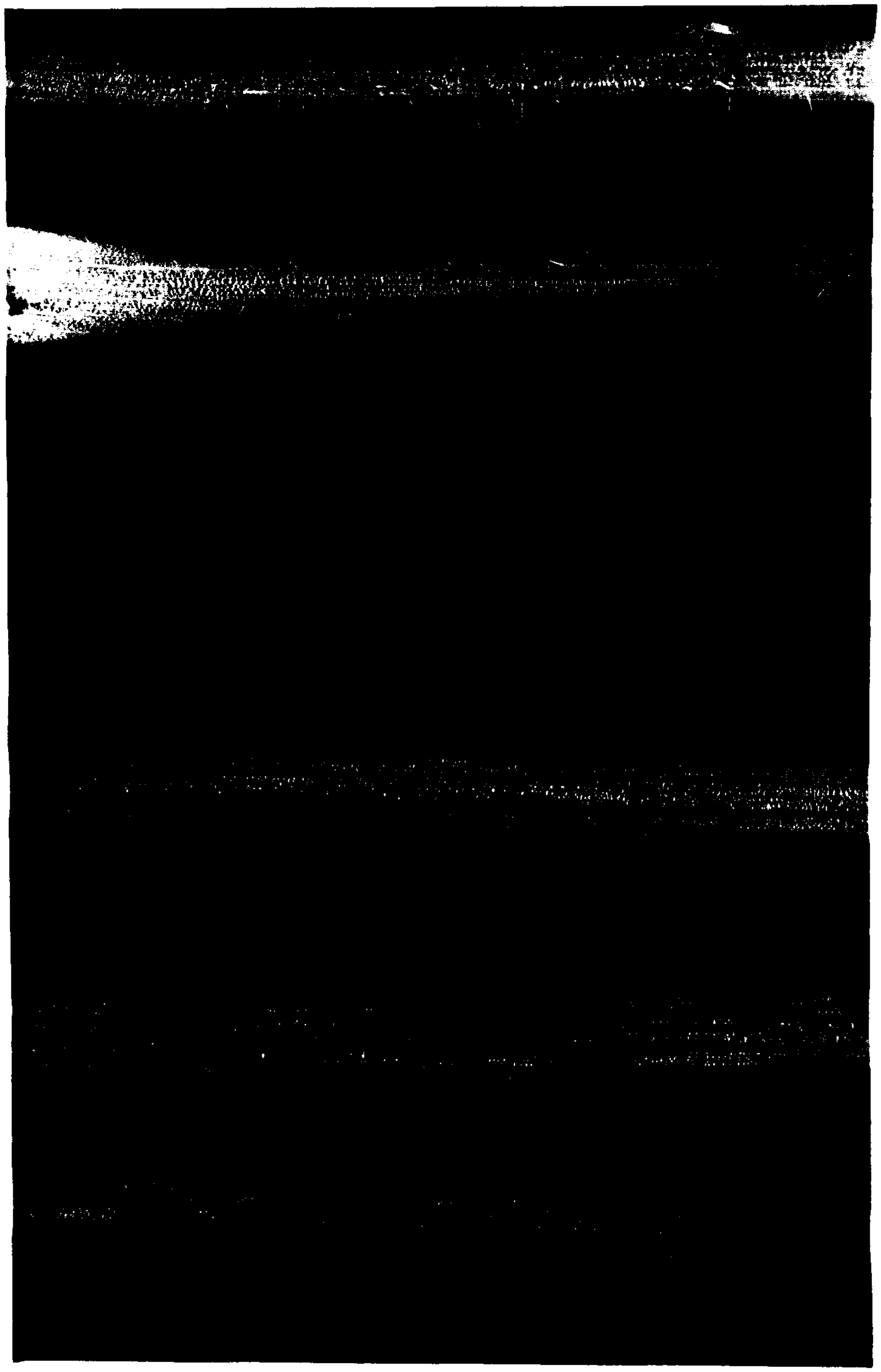


Figure 26. First leaf sheath pubescence of progeny of actual parents.

Left half. Variety Ukraine. Left to right. Plants 5-2, 5-3, 5-18 and 5-24.
Right half. Variety Landhafer. Left to right. Plants 6-2 and 6-23.

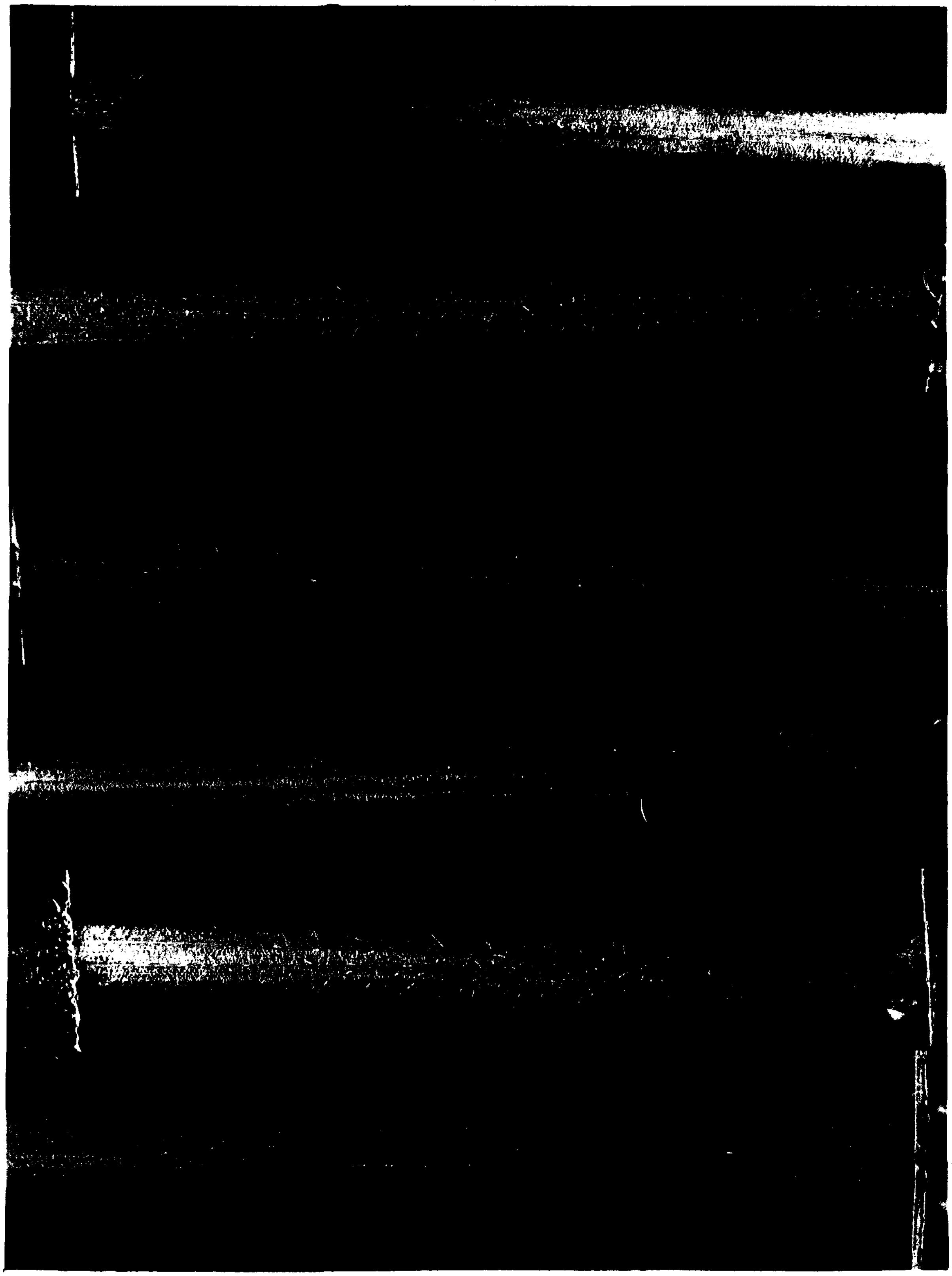


Figure 27. First leaf sheath pubescence of progeny of actual parents.

Left half. Variety Reselect Clinton. Left to right. Plants 7-21 and 7-163.
Right half. Variety Anthony-Bond x Boone. Left to right. Plants 14-2, 14-4 and 14-5220.

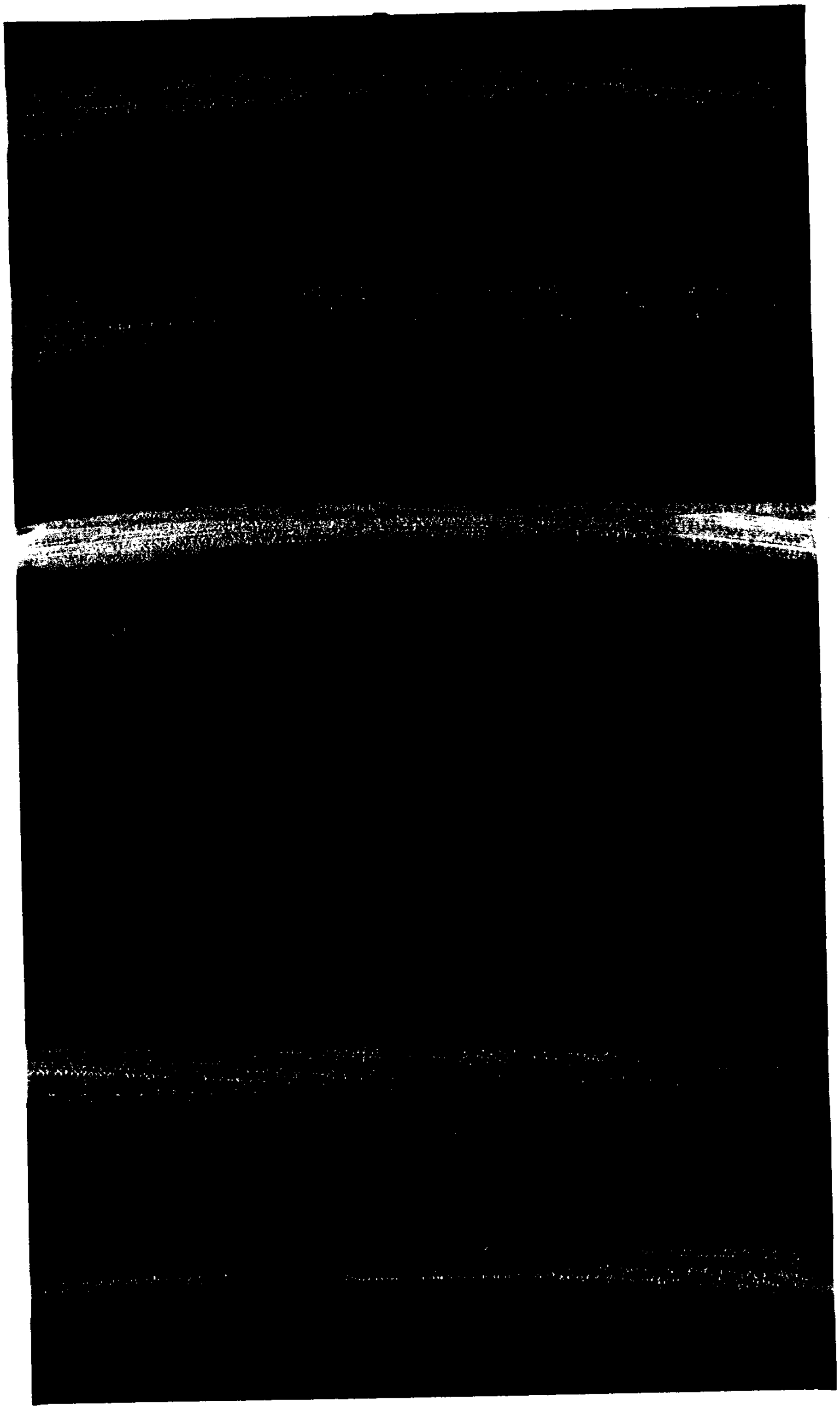
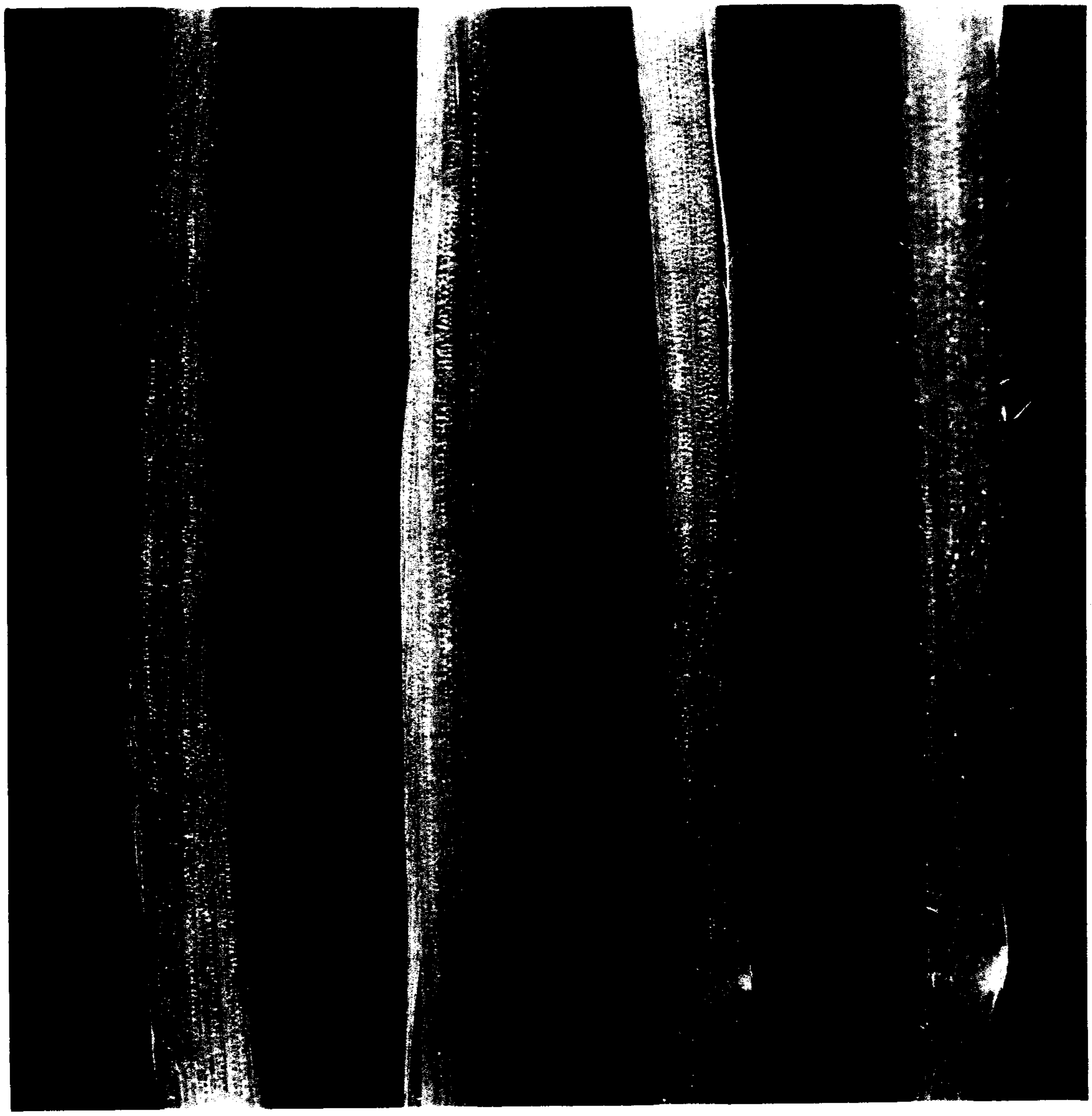


Figure 28. Example of classes used in classification of F_2 plants for extent of leaf sheath pubescence.

Left to right. Absent, few, several and many.



To interpret the data on a sound genetic hypothesis required a more intensive study than was possible. The readings were made on the leaf sheath of the first leaf. By holding the plant between a light source the hairs reflected the light making them visible. It was noted that seedlings showing no hairs on the first leaf sheath would in some cases show hairs on the second leaf sheath. There was considerable variation in the number, length and position of these hairs. The classification used was satisfactory within a cross but comparisons between crosses may not be valid. A more absolute classification system would be needed for a critical study.

It was evident that there was a genetic basis since the distribution of plants from a cross of absent x absent or few x absent had a concentration of F_2 seedlings in the classes few or absent. In crosses of many x several or many x many the concentration of individuals was in the many and several classes.

Inheritance of First Leaf Marginal Hairs

Inheritance of marginal hairs was studied in all crosses involving the variety Victoria as one parent. Victoria always showed hairs on the margin of the first leaf as well as the older leaves. Klein 69b and Landhafer showed none on the first leaf but usually some could be found on the older leaves. Marginal hairs were completely absent on Ukraine, Clinton and Anthony-Bond x Boone.

The F_2 seedlings were grouped into four classes as represented in Figure 29. The summarized data are presented in Table 31.

Figure 29. Example of classes used in classification of F_2 plants for extent of marginal hair production on the first leaf.

Left to right. Absent, few, several many.

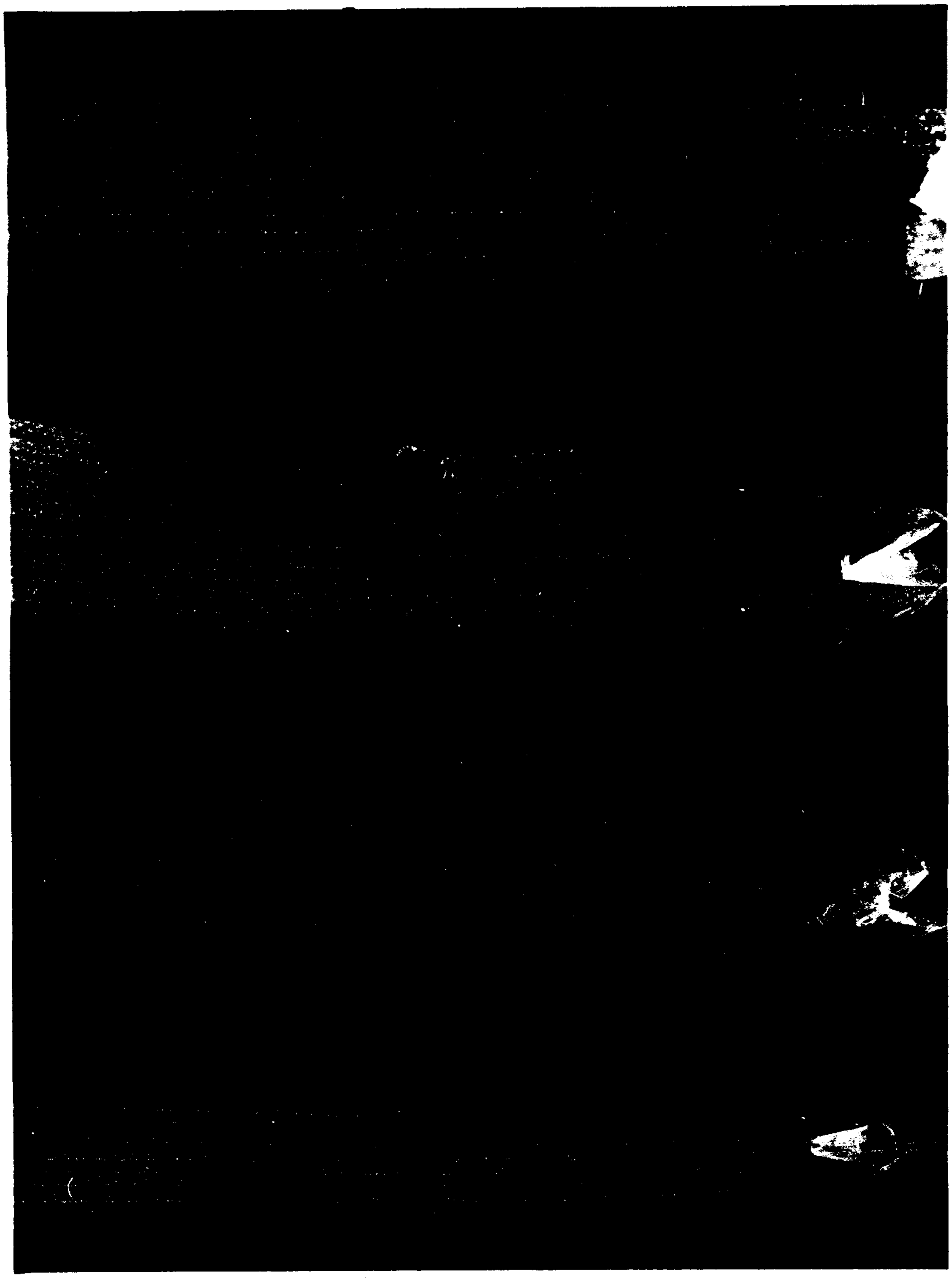


Table 31. F_2 segregation for extent of first leaf marginal hairs in five oat crosses.

	Cross[1]	Absent	Few	Several	Many	Total
69	Victoria x Klein 69b	67	18	2	6	93
30	Victoria x Ukraine	31	52	10	7	100
35	Victoria x (A.-B. x Boone)	79	22	1	7	109
34	Victoria x Clinton	116	13	2	2	133
33	Victoria x Landhafer	68	34	9	23	134

[1]Victoria parent - many first leaf marginal hairs.
Ukraine parent - no first leaf marginal hairs.
A.-B. x Boone - no first leaf marginal hairs.
Clinton parent - no first leaf marginal hairs.
Landhafer parent - no first leaf marginal hairs.

Classification was according to the first leaf only, but it was often noticed that plants having none or few marginal hairs on the first leaf would show a greater number on older leaves. The hairs varied in number, size and distance between hairs.

The data of Victoria x Klein 69b, Victoria x Ukraine and Victoria x (Anthony-Bond x Boone) would fit a two factor hypothesis assuming two partially dominant factors which inhibit the production of marginal hairs. The data from the cross Victoria x Clinton would fit a three factor hypothesis with the same gene action as above. The data from Victoria x Landhafer appear to differ by a single factor using the same assumptions.

While the above hypotheses were not at all unreasonable, the F_2 data do not afford conclusive proof of a hypothesis made up from the results of the same population.

Notes Concerning Albino Plants

The occurrence of albino plants has been reported in many species of plants. The frequency of albino plants is generally lower in the polyploid species of plants and occur generally in advanced generations of hybrid populations. Albino plants in this study appeared in the F_3 generation in 8 of the 24 crosses advanced to the F_3. A summary of F_3 lines segregating for albino and normal plants is given in Table 32.

All except two of the crosses had Ukraine as one parent. This fact may indicate genes conditioning albino plants were present in some of the original parents rather than resulting from mutation. No albino

Table 32. Summary of occurrence of albino seedlings.

Cross No.	F_3 line	Albino	Normal	Female parent	Male parent
11	28	1	18	1-26	5-3
76	023	2	3	5-18	2-12
76	050	3	16	5-18	2-12
76	054	5	24	5-18	2-12
76	075	25	5	5-18	2-12
76	14	13	7	5-18	2-12
30	7	21	5	5-24	3-11
30	V412	1	3	5-24	3-11
39	09	1	5	5-3	4-11
39	050	3	2	5-3	4-11
88	31	3	26	4-16	6-23
88	230	3	17	4-16	6-23
48	116	1	8	4-3	14-6
56	01	17	21	5-2	14-4
40	15	3	2	5-3	4-11

plants were observed in the F_2 from any of the crosses. If the genes conditioning albinoism were present in the parents it should be possible to produce albino plants in the F_2 generation. The low frequency of albino plants even in the F_3 indicated complicated gene action which would be difficult to distinguish from mutation frequencies which produce albino plants.

DISCUSSION OF EXPERIMENTAL RESULTS

A summary of the proposed genotypes of the parental varieties used in this study is shown in Table 33[1]. It must be realized in some cases the data were not extensive or complete enough from any one cross to correctly identify the genotypes of the parental varieties. However, each cross provided critical information and a critical test of every other cross. Any hypothesis that can explain the results of all crosses is probably correct even if an unsatisfactory fit to statistically calculated numbers is obtained for any one cross. The breeding behavior of varieties in diallel crosses of several varieties provides a more critical test of any hypothesis than a statistical test for goodness of fit for each individual cross, especially where the amount of data for any one cross may be small.

This study was designed with the assumption that crown rust reaction was Mendelian in nature and that the parental materials (varieties and individual plants within a variety) were homozygous for their particular type of crown rust reaction. The results of this study indicated the assumption of homozygosity of varieties may have been incorrect. The origin of many of the parental varieties is not definitely known. It is quite reasonable to assume that the parents used in this study were not descendent from a single homozygous plant. Therefore, even if selection for crown rust type had been practiced it is unlikely

[1]The actual data recorded during this investigation are filed at Iowa State College. They may be obtained by written request from Farm Crops, Department of Agronomy, Iowa State College, Ames, Iowa.

Table 33. Proposed genotype of parental varieties used in the investigation of inheritance of resistance and susceptibility to crown rust race 57.

Klein 69b	KK	mm	uu	vv	ll	$i_k i_k$
Trispernia	kk	M_2M_2	--	--	ll	$i_k i_k$
Victoria	kk	mm	uu	VV	ll	$i_k i_k$
Santa Fe	kk	M_1M_1	uu	vv	ll	$i_k i_k$
Ukraine	kk	MM	UU	vv	ll	$i_k i_k$
Landhafer	kk	mm	uu	vv	LL	$i_k i_k$
Reselect Clinton	kk	mm	uu	vv	ll	$I_k I_k$
Anthony-Bond x Boone	kk	M_2M_2	--	V_1V_1	ll	$i_k i_k$

that all plants would be of the same genotype since the data indicated the presence of duplicate factors in some of the varieties.

The rust reaction of Klein 69b was uniform, at least for the plants used as parents. The field reaction was uniform but differed from the greenhouse reaction in that the adult plants in the field showed a very high type of resistance. Under an extremely heavy artificial rust epiphytotic the adult parental plants had a 0 type reaction. No crown rust pustules were observed on these plants.

The rust reaction of the parental plants of the variety Trispernia varied in the field as they did in the greenhouse. Parent 2-23 was the least resistant, 2B-27 intermediate and the others the most resistant. This relationship held for the adult plants in the field, however a higher type resistance was shown in the field than in the greenhouse. Different genotypes of plants within this variety have been used to explain the results. It would not be surprising if the variety Trispernia contained plants with the genotype for resistance to crown rust race 57 of $M_2M_2U_2U_2V_1V_1$ or any homozygous combination of one or two factor pairs. A great deal of variation has been observed in the crown rust reaction of the variety Trispernia when it is used as a differential variety. The proposed hypothesis would account for this variation.

Although the reaction of plants from the variety Victoria was fairly uniform, a great deal of variation occurred in the reaction of the Victoria gene in segregating generations. The Victoria gene may have been only partially dominant, there may have been a considerable environmental effect, or there may have been a considerable gene background effect.

The Victoria type reaction was subdivided into groups based on varying amounts of pustule formation. Many plants showed no pustules while others were classified as fully susceptible and others at various intermediate levels. All of these plants contained the Victoria gene for crown rust resistance as shown by their susceptibility to _H. victoriae_. The environment did not produce all the effect since F_3 plants growing in the same pot showed all degrees of pustule formation. The heterozygous condition was in general a lower type of resistance than the homozygous condition, but this does not explain all the variation since some true breeding lower Victoria types of resistance were found. It is necessary to assign a great deal of the variation to gene background effect.

Since the Victoria type of crown rust reaction is distinct from the other types, it is interesting to speculate on why it differs. The theory of ultrasusceptibility, i.e., the Victoria type is so susceptible that entrance of the pathogen so rapidly kills the host cells that little or no sporulation occurs, thus the host is resistant, has been proposed by many investigators. Litzenberger (12, pp. 476-477) in crosses of Mindo x Victoria to determine the inheritance of race 1 of crown rust stated:

> Factorial analysis presented in table 6 assumes that A and B are complementary and V is expressed only when in presence of germ plasm susceptible to _P. coronata avenae_. That is, when A and B are present to give the Bond type of resistance the fungus is prevented from developing to the sporulation stage, when tissue collapse (conditioned by V) normally begins.

The data of this study supports his conclusions that the Victoria type reaction is not expressed in the presence of other factors giving an immune or O type reaction, but the conclusion that V is expressed only in susceptible germ plasm is not in agreement with results of thie investigation; unless the Victoria gene is a gene for susceptibility. In the crosses of Victoria with resistant parents Klein 69b and Anthony-Bond x Boone the Victoria type of reaction was expressed in resistant germ plasm to race 57 as shown in Tables 14 and 15. There is no way to determine whether this Victoria gene conditions a resistant or a susceptible reaction (resulting in a resistant classification). Either way it is intermediate on the scale of dominance or epistasis in relation to other genes for crown rust resistance to race 57. The nature of resistance to crown rust is unknown but it is quite conceivable that a gene may condition resistance to one race of crown rust and susceptibility to another race.

In all Santa Fe parents, except one, a single factor pair was assumed to govern the Santa Fe type of crown rust resistance to race 57. The single factor pair was assumed to be allelic to one of the two linked Ukraine factor pairs for resistance. Santa Fe parent 4-3 was assumed to carry alleles to both of the Ukraine factors. It is well known that the reaction of Santa Fe is variable when used as a differential variety. Possibly the Santa Fe variety is a mixture of genotypes for crown rust resistance some plants have the genotype $M_1M_1U_1U_1$ some M_1M_1 or some U_1U_1.

The variety Ukraine was assumed to have the genotype MMUU, the genes being linked. A crossover value of 23 percent was estimated from the cross of Ukraine x Clinton. A better estimation of linkage may be made by the use of data from other crosses with Ukraine. A summary of the data used and the estimation of percent crossing over with its standard error are given in Table 34.

Table 34. Estimation of linkage intensity of duplicate genes, controlling resistance to crown rust race 57, in the variety Ukraine from corrected F_2 data.

Cross	Corrected F_2 data: Bred true Ukraine type	Segregated parental types	Bred true other parent	Total	Maximum liklihood estimate of recombination
Ukraine x					
Trispernia	44	60	12	116	
Santa Fe	52	70	26	148	
A.-B. x Boone	17	36	10	63	
Clinton	50	67	21	138	
Total	163	233	69	465	22.8 ± .04

All data from crosses involving Landhafer as one parent showed the Landhafer type of resistance was conditioned by a single factor pair.

All data from crosses involving Reselect Clinton indicated that Clinton carried only recessive alleles to factors for resistance except in the case of Clinton x Klein 69b. The data here suggested Clinton carried a dominant inhibitor factor which was epistatic to the Klein 69b gene for crown rust resistance. It is quite possible that this inhibitor gene was part of the gene background which contributed to the variation in the Victoria type of reaction. Such genes also may explain why classification was so difficult in crosses of varieties having a low type of resistance with susceptible Clinton. This gene may affect the lower type of resistance more than a higher type of resistance. The presence of such genes may seriously handicap a backcross breeding program where an attempt is made to transfer a gene for resistance to a susceptible variety by using the susceptible variety as the recurrent parent.

The data concerning the Anthony-Bond x Boone parents indicated their genotypes were probably the same. The actual parent used in the cross with Reselect Clinton was not available for study. The parent was from the variety C.I. 5220 and plants from this variety did not show as high a type of resistance as did the progeny of the other actual parents. All Anthony-Bond x Boone progenies showed a higher type of resistance in the field than they did in the greenhouse.

The data from this study indicated at least 8 genes at five loci were involved in determining resistance and 1 gene (other than recessive) determining susceptibility to crown rust race 57. Even with only 5 loci (more are known and probably many more exist) 31 combinations of one or more of these genes at separate loci in the homozygous condition could be obtained. It would be very desirable to have available all of these combinations but the mechanics of isolation, for even one race of crown rust, are so difficult that the desirability may not be realized. The solution of the problem then becomes one limited by practicability.

The immediate breeding program should then be directed toward the development of varieties containing the single genes governing resistance to most of the races followed by the most simple combinations to the more complex combinations. The major limitations of such a program are (1) It is not known for certain which genes condition resistance to specific races. (2) A resistant variety provides a selection pressure against races of rusts, eliminating those to which it is resistant, thus only those races (new recombinations, mutations, or present unidentified races) to which the variety is susceptible can survive. The amount of selection pressure is a function of the total oat acreage devoted to varieties containing this particular gene.

The first limitation can be solved by experimental research. The solution to this problem is now under way at Iowa State College and at other institutions. It is the second limitation that causes the most concern.

Sources of resistance are available to all known races at the present time. Some varieties or selections are resistant to all races to which they have been exposed. It is quite likely that a gene or combination of genes for resistance can be found that will give resistance to any one race of crown rust. However, it may take considerable time to develop a suitable variety with the desired combination of genes. It may be unwise to release varieties having genes from all sources of resistance at one time because of the danger that selection pressure may produce a race that would parasitize all varieties. It is also unwise to have the entire oat acreage planted to one variety. The best procedure would be to use the fewest genes or combination of genes which will control the prevalent races of crown rust. These genes should be placed in several acceptable varieties of diverse germ plasm. Genetic stocks of genes and combination of genes for resistance to crown rust should then be built up and be available for transfer to desirable varieties. Using a backcross breeding program, the transfer of genes could be accomplished and the variety released before a new race of rust could be a serious threat to the old variety. The success of such a program would depend upon the early identification of new rust races. This should not be difficult since the varieties themselves are the only differentials needed for the first identification of new races.

The major sources of resistance now available and a summary of their host-parasite relationships are given in Table 35. To best utilize these sources of resistance it is necessary to know the number of genes and the gene action involved in resistance to each of these races of crown rust.

For crown rust race 57, resistance was partially dominant to susceptibility. The higher the type of resistance the higher was the phenotypic dominance for resistance. The same relationship held for epistasis and/or dominance between and among genes for resistance.

The genes for resistance as designated in Table 33 had the following relationships:

1. M, U or MU epistatic or dominant to all other genes tested.
2. M_1 or L epistatic or dominant to other genes except M_1 U or MU.
3. V dominant to V_1 and epistatic to K.

The gene I_k for susceptibility was epistatic to K. There may be minor differences in other relationships between and among these genes but they have not as yet been clearly established, i.e. the degree of resistance of M and U or of M_1 and L may not be exactly the same, or I_k may lower the resistance level of some or all of the genes.

[1]Table 35 and data presented in footnotes were summarized from Murphy (16).

[2]The reaction of Landhafer has not been recorded to crown rust races 8, 10, 13, 16, 19, 21, 23, 24, 27, 30, 32, 36, 37, 39, 44 and 55.

[3]The reaction of Santa Fe has not been recorded to crown rust races 2, 3, 5, 8-10, 13, 14, 16-19, 21, 23-25, 27, 28, 30-32, 35-39, 41-44, 50, 52, 53, 55, 58, 62-67, 70-72, 74-76, 79, 80, and 84-86 incl.

[4]The reaction of Victoria has been recorded for all 95 races.

[5]The reaction of Bond has been recorded for all 95 races.

[6]The reaction of Anthony-Bond x Boone has been recorded only to races 1, 6, 7, 11, 22, 33, 34, 40, 45, 46, 48, 49, 51, 56, 57, 59, 60, 68, 69, 73, 77, 78, 81-83 and 87-95 incl.

[7]The reaction of Trispernia has not been recorded to the same races as shown above for Santa Fe.

[8]The reaction of Ukraine has not been recorded to crown rust races 5, 8-10, 13, 14, 16-19, 21, 23-25, 27, 28, 30-32, 35-37, 39, 42, 44, 50, 52, 53, 55, 58, 62-66, 70, 72, 74-76, 79 and 85.

[9]The reaction of Klein 69b has been recorded only to races 1, 6, 7, 22, 33, 34, 50, 45, 46, 48, 49, 51, 56, 57, 59, 60, 68, 69, 73, 78, 81-83, 87 and 88.

Table 35. Oat varieties susceptible in seedling stage to specific races of crown rust identified among collections obtained throughout the United States in 1930 to 1949.[1]

Variety or selection	C.I. No.	Tested with races collected in-	Susceptible to races-
Landhafer[2]	3522	1938-1949 incl.	none
Santa Fe[3]	4519	1947,1948,1949	none
Victoria[4]	2401	1930-1949 incl.	41, 50, 52, 53, (55) & 56
Bond[5]	2733	1930-1949 incl.	33, 34, 45, (55), 57, 68, 69, 87, 88, 89, 90, 91, 92, 93, 94 & 95
Anthony-Bond x Boone[6]	5401	1948-1949	Biotypes of 45, 57 & 68
Trispernia[7]	4009	1947,1948,1949	Biotypes of 45, 57, 68 69, 82 and 88
Ukraine[8]	3259	1946-1949 incl.	Biotypes of 1, 6, 11, 15, 45, 47, 48, 54, 57, 60, 68, 69, 82, 88, 90, 91, 92 & 93
Klein 69b[9]	4118	1948	Biotypes of 1, 45, 57, 68, 78 and 88

The reason for epistasis or dominance for resistance is understandable, for example in the extreme case of immune type of resistance vs. any other type of crown rust reaction: if the genes controlling immunity are present, the fungus is killed before it can develop sufficiently to give some other type of reaction. The type of reaction depends upon the degree of development of the pathogen on the host; resulting in epistasis when contrasting factors are present.

The different types of reactions to different races of rust will be very useful in the identification of genes for the development of genetic stocks of different gene combinations.

Breeding for crown rust resistance in oats is a complex problem and the most efficient method will be the one based on a known genetic basis.

SUMMARY

Corrected F_2 data from 23 oat crosses involving 8 major sources of resistance to crown rust were interpreted in determining the inheritance of resistance and susceptibility to crown rust race 57.

The varieties used as parents and their assigned genotypes were as follows:

1. Klein 69b - Resistant - KK mm uu vv ll $i_k i_k$
2. Trispernia - Resistant - kk $M_2 M_2$ -- -- ll $i_k i_k$
3. Victoria - Resistant - kk mm uu VV ll $i_k i_k$
4. Santa Fe - Resistant - kk $M_1 M_1$ uu vv ll $i_k i_k$
5. Ukraine - Resistant - kk MM UU vv ll $i_k i_k$
6. Landhafer - Resistant - kk mm uu vv LL $i_k i_k$
7. Reselect Clinton - Susceptible - kk mm uu vv ll $I_k I_k$
8. Anthony-Bond x Boone - Resistant - kk $M_2 M_2$ -- $V_1 V_1$ ll $i_k i_k$

The interallelic and intrallelic gene action was as follows:

1. M, U, or MU epistatic or dominant to all others.
2. M_1 or L epistatic or dominant to others except M, U, or MU.
3. V dominant to V_1 and epistatic to K.
4. $I_k I_k$ epistatic to K.

The genes designated as M and U were linked in the coupling phase with 22.88$\pm$.04 percent recombination.

Inheritance of reaction to *H. victoriae* was shown to be monogenic with susceptibility dominant and completely linked with the Victoria type of crown rust resistance.

A hypothesis of two partially dominant complementary factor pairs

was advanced to explain the occurrence of dwarf plants in the F_2 generation from normal parents and F_1.

A relationship was shown between the Ukraine type of resistance to crown rust race 57 and susceptibility to an unidentified isolate of crown rust which attacks Ukraine.

Inheritance of pubescence of the first leaf sheath and of marginal hairs on the first leaf was studied. The mode of inheritance was not placed on a factorial basis.

The application of the information obtained from this study in a program of breeding oats resistant to crown rust was discussed.

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